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THE ECOLOGICAL RELATIONS OF THE VEGETATION ON THE SAND DUNES OF LAKE MICHIGAN

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BY

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THE ECOLOGICAL RELATIONS OF THE VEGETATION ON THE SAND DUNES OF LAKE MICHIGAN.

PART I.—GEOGRAPHICAL RELATIONS OF THE DUNE FLORAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XIII.

HENRY CHANDLER COWLES.

(WITH FIGURES 1–26)

I. Introduction.

THE province of ecology is to consider the mutual relations between plants and their environment. Such a study is to structural botany what dynamical geology is to structural geology. Just as modern geologists interpret the structure of the rocks by seeking to find how and under what conditions similar rocks are formed today, so ecologists seek to study those plant structures which are changing at the present time, and thus to throw light on the origin of plant structures themselves.

Again, ecology is comparable to physiography. The surface of the earth is composed of a myriad of topographic forms, not at all distinct, but passing into one another by a series of almost perfect gradations; the physiographer studies landscapes in their making, and writes on the origin and relationships of topographic forms. The ecologist employs the methods of physiography, regarding the flora of a pond or swamp or hillside not as a changeless landscape feature, but rather as a panorama, never twice alike. The ecologist, then, must study the order of succession of the plant societies in the development of a region, and he must endeavor to discover the laws which govern the panoramic changes. Ecology, therefore, is a study in dynamics. For its most ready application, plants should be found whose tissues and organs are actually changing at the present time in

response to varying conditions. Plant formations should be found which are rapidly passing into other types by reason of a changing environment.

These requirements are met *par excellence* in a region of sand dunes. Perhaps no topographic form is more unstable than a dune. Because of this instability plant societies, plant organs, and plant tissues are obliged to adapt themselves to a new mode of life within years rather than centuries, the penalty for lack of adaptation being certain death. The sand dunes furnish a favorable region for the pursuit of ecological investigations because of the comparative absence of the perplexing problems arising from previous vegetation. Any plant society is the joint product of present and past environmental conditions, and perhaps the latter are much more potent than most ecologists have thought. As will be shown in another place, even the sand dune floras are often highly modified by preexisting conditions, but on the whole the physical forces of the present shape the floras as we find them. The advancing dune buries the old plant societies of a region, and with their death there pass away the influences which contributed so largely to their making. In place of the rich soil which had been accumulating by centuries of plant and animal decay, and in place of the complex reciprocal relations between the plants, as worked out by a struggle of centuries, the advance of a dune makes all things new. By burying the past, the dune offers to plant life a world for conquest, subject almost entirely to existing physical conditions. The primary motive, then, which prompted this present study was the feeling that nowhere else could many of the living problems of ecology be solved more clearly; that nowhere else could ecological principles be subjected to a more rigid test.

This particular investigation was also prompted by the fact that the previous ecological studies of sand-dune floras have been carried on chiefly in European countries, and almost exclusively along marine coasts. There has been considerable difference of opinion as to the influence of salty soils and atmospheres upon the vegetation. It would seem that a comparison of dunes

along an inland fresh water lake with those along the sea should yield instructive results.

An ecological study of this character has a natural twofold division. In the first place the plant formations are to be investigated. The species characteristic of each formation must be discovered, together with the facts and laws of their distribution. The progressive changes that take place and the factors in the environment which cause these changes must be discussed. This phase of the subject is largely geographic, and will be the special feature of the present paper. In another paper it is the author's purpose to discuss the adaptations of the plants to their dune environment, paying especial attention to those species which show a large degree of plasticity, and which are found growing under widely divergent conditions. This second phase again has a natural twofold division, one part treating of gross adaptations such as are shown in plant organs and plant bodies, the other dealing with the anatomical structures of the plant tissues.

The material for the present paper has been gathered chiefly from the study of the dunes in northwestern Indiana in the vicinity of Chicago. These studies were carried on in the seasons of 1896, 1897, and 1898, frequent visits being made to various points at all seasons of the year. A portion of the summer seasons of 1897 and 1898 was spent in a more rapid reconnoissance along the entire eastern shore of Lake Michigan, including the group of islands toward the north end of the lake.

The work resulting in this paper has been carried on in connection with the Hull Botanical Laboratory of the University of Chicago, and the author gratefully acknowledges the kindly interest and cooperation shown by his associates among the faculty and students of the botanical department, especially Head Professor John M. Coulter, through whose influence the author was directed along lines of ecological research. The author further desires to express his great indebtedness to Dr. Eugen Warming, professor of botany at Copenhagen; his textbook on ecology and his treatises on the sand-dune floras of

Denmark have helped greatly to make clear the true content of ecology, and they have been a constant incentive to more careful and thorough work. Most of the photographs were taken especially for this paper by Mr. E. W. Martyn, a Chicago photographer. Some of the views were taken by Messrs. S. M. Coulter and H. F. Roberts, students in the Hull Botanical Laboratory. The map was prepared by Mr. S. M. Coulter.

II. General features of the coast of Lake Michigan.

Along the eastern shore of Lake Michigan there are hills of wind-blown sand almost continuously fringing the border of the lake. This line of sand hills also continues around the southern end of the lake and along the western shore as far as Chicago. These sand hills or sand dunes form striking topographic features in the landscape, and in this respect present a strong contrast to the level prairies or fields beyond.

Geologically speaking, the sand dunes belong to the most recent formations, as they are entirely post-glacial. In most cases the origin of the existing topographic forms is to be referred to the most recent phases of post-glacial history, and in many instances the topographic forms are either being made or unmade at the present time. As a rule the dunes are directly superposed upon the beach. On the northeastern shores of the lake, however, the dunes are commonly superposed upon bluffs of clay or gravel, sometimes 120 meters above the present beach.

In the lake region there is a decided prevalence of westerly winds, chiefly from the southwest or northwest. As a consequence, the dunes are found along the entire eastern and southern shores of the lake, whereas the dunes on the western shore, due to easterly winds are merely small hillocks of sand. Such small dunes have been seen at Waukegan, Ill., and on North Manitou and Beaver islands. The dunes toward the southern portion of the lake were created and fashioned, as a matter of necessity, almost entirely by the northwest winds. In order to secure any extensive formation of sand dunes, it is necessary for the wind to gather force by sweeping over the lake and to strike the coast

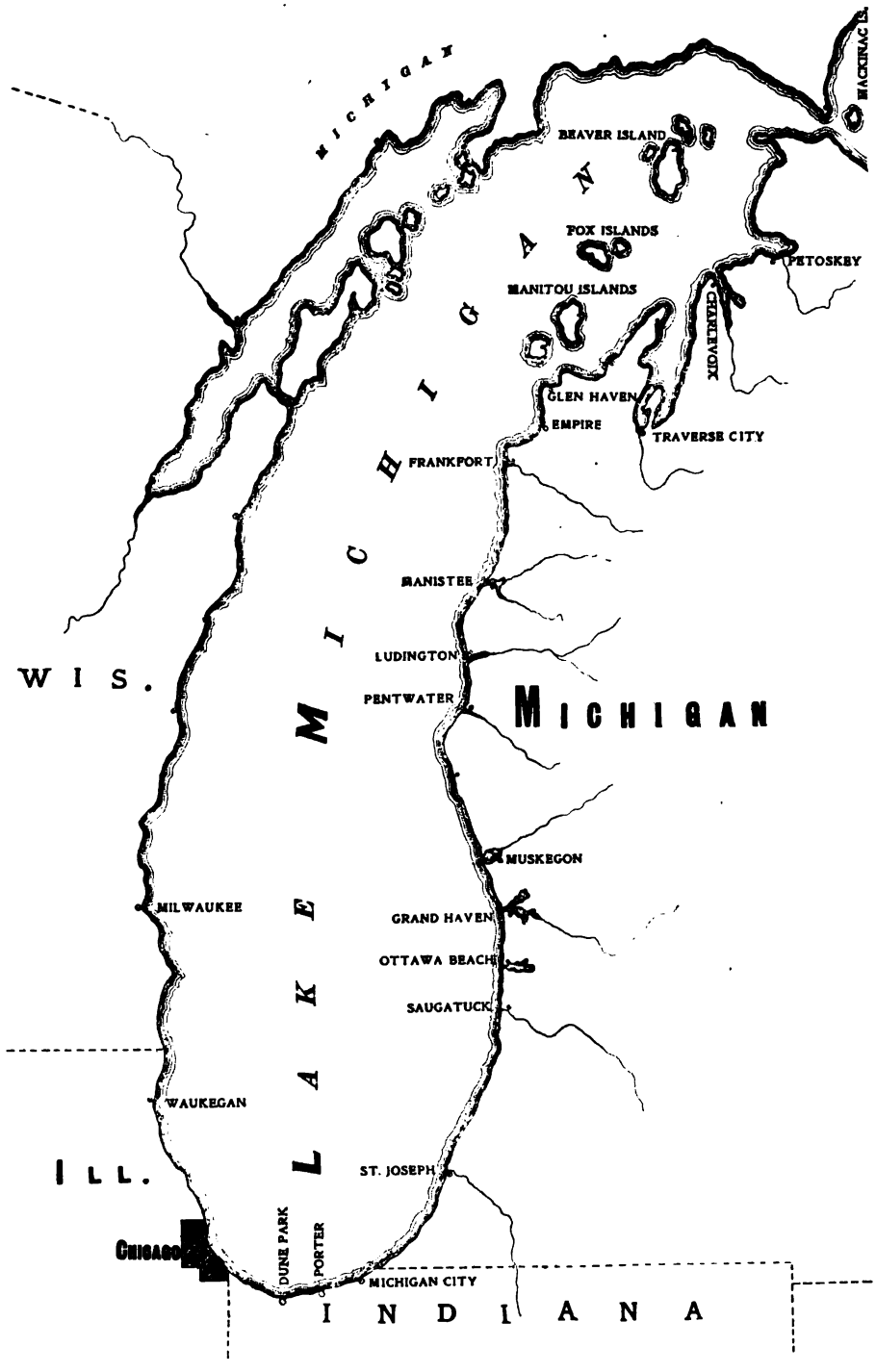

FIG. 1.—MAP OF THE SHORE OF LAKE MICHIGAN. SCALE, 1:2,850,000.

almost at right angles to the shore line. It will thus be seen that the most favorable theoretical locality for dunes in a region of northwest winds is on the southeast shore of a body of water in that region. As a matter of fact, the dune region increases in area and the dunes themselves increase in height and complexity as one passes from Chicago around the south end of Lake Michigan. The culmination of the dune formations actually occurs between Dune Park and Michigan City, and an examination of the accompanying map (*fig. 1*) will show that these localities have a shore line running nearly southwest to northeast. The contour of the dunes themselves also shows that they were shaped by northwest winds, as does the path formed by the sweeping of the wind.

The Dune Park region furnishes the most extensive area of present dune activity to be found along the southern coast of Lake Michigan, although the altitudes of individual dunes are much greater at many points in Michigan. Elsewhere the active dunes are usually confined to a very narrow belt fringing the shore, but at Dune Park the dunes are active from one to two kilometers inland, the front of the advancing dunes varying from 6 to 30 meters in height. The dune complex or area of dune activity at Dune Park covers perhaps 1000 hectares. The established dunes here as elsewhere cover a far greater area than do the active dunes, reaching inland three to eight kilometers. Between Chicago and Dune Park there is a most interesting series of parallel ridges, alternating with depressions, which often reach below the water level throughout the entire year. The origin of these ridges is scarcely within the province of this paper; their extreme regularity of contour, in addition to their persistent parallelism, seems hardly consonant with a dune origin. Because of the low altitude of these ridges and their protection from shore conditions, their flora is not typically xerophytic. Whatever the origin of these ridges, they represent a phase in the lake's history when its waters were much farther inland than at present. The active dunes at Dune Park are scarcely ever more than 30 meters in altitude, but there are

several established dunes which are more than 36 meters above the lake. The coast charts issued by the Corps of Engineers of the United States War Department figure a dune near Porter, Ind., which reaches an altitude of 57 meters above the lake. Of course, altitudes of individual dunes are subject to much change, although in the case of established dunes the figures need but slight revision. The highest series of dunes is along the Michigan shore between Michigan City and St. Joseph. A large number of dunes reach an altitude of more than 60 meters; several are over 90 meters high; and one is figured on the coast chart which has an altitude of 117 meters above the level of the lake. An inspection of the map will show that these dunes must have been shaped primarily by northwest winds.

The Michigan shore between St. Joseph and Frankfort, a distance of more than 250 kilometers, is fringed almost continuously with a narrow belt of dunes. Perhaps at no place within this region are there such extensive dunes in activity at the present time as at Dune Park, nor do the established dunes reach inland as a rule for more than a kilometer. At Dune Park there is a gradation in the altitude of the dunes as one goes inland, until the low sand ridges pass all but insensibly into the prairies beyond. Along the Michigan shore, however, there is a narrow fringe of dunes close to the lake, commonly much higher than at Dune Park, and the transition between these dunes and the normal inland country is rapidly passed and plainly marked.

A very striking feature along the Michigan shore is the tendency of rivers to form small lakes near their mouths. These lakes determine the presence of cities, since they furnish the best of harbors. An inspection of the map (*fig. 1*) shows the presence of such natural harbors at the mouths of rivers at Holland (Ottawa Beach), Grand Haven, Muskegon, Whitehall, Pentwater, Ludington, and Manistee. A large amount of the silt brought down by the rivers is deposited at the mouth, where the river currents are slackened by their opening out into the lake and by wave action. The waves pile up this sand along the beach and the winds pick it up and form extensive dunes at the

river's mouth. All along the Michigan coast the most extensive areas of active dunes are likely to be at the mouths of the rivers, so that dune formation is thus seen to be regulated by the supply of sand as well as by the relation of the coast line to the direction of the prevailing winds. Since the general direction of the Michigan coast line is north and south, and the prevailing winds southwest and northwest, dune formation tends to close up the mouths of the rivers on both sides. The result of this conflict between the river and air currents is seen in the formation of lakes whose entrance into Lake Michigan is constricted into a narrow passageway. The tendency of the wind to close these passageways is so great that navigation is often difficult, and the necessity for constant dredging and erection of windbreaks is obvious.

The dunes at the mouths of rivers furnish a rough measure for determining the relative influence of northwest and southwest winds in dune formation, since those on the south side are largely shaped by southwest winds and those on the north side by northwest winds, although each wind modifies the action of the other. At Saugatuck the southwest winds appear to dominate, since the dune south of the river is 78 meters high, while to the north the heights are inconspicuous. The course of the Kalamazoo river has been deflected to the northward at this point, although it is interesting to observe that the mouth is now being deflected to the southward, the river filling in on the northwest bank and eroding on the southeast. At Ottawa Beach the dunes are about equal on both sides, and less than 60 meters in height. At Grand Haven there is an immense active dune on the north side of the river, 66 meters high, and with an advancing lee slope 45 meters in height. This dune is deflecting the river to the southward, and attempts to stop its progress are not particularly successful. The dunes at Muskegon are largest on the south side of the river. At Pentwater, Ludington, and Manistee the dunes average about 45 meters in height. The fringe of dunes is interrupted at several points by clay bluffs, but this latter formation is far more extensive farther northward.

Active dune formation is conspicuous on projecting points of land as well as at the mouths of rivers; for example, active dunes are to be found on Little Point Sable, south of Pentwater, and Big Point Sable, north of Ludington. At many points along the coast the winds are breaking through the fringe of established dunes, so that the older dunes may be said to have started into activity again or to have become rejuvenated. In summation concerning the area between St. Joseph and Frankfort, it may be said that the influence of northwest and southwest winds in dune formation is nearly equal. Indeed, the two winds commonly work together to produce a composite result, so that the winds sweep and the dunes advance, as a rule, from west to east.

In northern Michigan, between Frankfort and Glen Haven, and also on North Manitou island, most of the dunes are perched high up on bluffs of clay or gravel. The bluffs are steep and approach the water's edge, varying in height from nothing up to more than 120 meters. Dunes are to be found upon the tops of the very highest of these bluffs in the district south of Glen Haven. These perched dunes are almost wholly established, and it seems as if their formation took place years ago when the lake was perhaps at a higher level. The most remarkable dune formation along the entire coast of Lake Michigan is to be found on Sleeping Bear point, just south of Glen Haven. The point stretches out into the lake, and is constantly growing to the northward and eastward by reason of the joint action of waves and winds. The point proper is geologically quite young, and, apart from the present beach and stationary beach dunes, is covered by an immense and active dune complex. At many points the wind has scooped out great hollows in the complex, exposing the gravel of a former beach. The advance of the dunes in this area is chiefly eastward, the exposed fossil beaches being chiefly toward the west. Two or three kilometers southward from the point, the region of low active dunes passes somewhat suddenly into an immense flat-topped hill, rising abruptly from the lake like a mesa or terrace. The height of the dunes on the point is seldom greater than 30 to 45 meters, while this peculiar

gravel terrace, or mesa, has an average height of 120 meters above the lake level, and an area of more than 2000 hectares, since it extends inland for about two kilometers, and along the coast for, perhaps, 15 kilometers. The Sleeping Bear itself, which gives its name to the point, and also to the bay, is a long established dune, with an altitude of 30 meters above the terrace on which it stands, or 150 meters above the lake. This dune stands alone, and is a landmark for miles in all directions. Farther to the south, dunes are perched upon these bluffs almost continuously, and there are reasons for supposing that the Sleeping Bear is but the last remnant of such a chain of dunes formerly superposed on the bluffs near Glen Haven. Toward the east and north, as well as toward the lake, the slopes of the mesa-like formation are quite abrupt, and beyond these slopes there is to be found an extensive dune complex, the grandest in variety and beauty to be found along Lake Michigan. It seems almost certain that the source of the sand for this dune complex was an ancient row of dunes at the top of the mesa toward the west. This is made more probable by the fact that the Sleeping Bear, once firmly established, is now being torn up by the winds and carried northeastward. The dune complex is moving toward the east, the line of advance being parallel to the lake shore, as usual. This advancing dune is far and away the grandest along Lake Michigan, presenting an almost continuous front, measuring four kilometers from north to south, all in active progression. The average height above the country on which it is encroaching is about 60 meters, so that it presents a most imposing sight when viewed from the fields in front of its line of advance. The dune complex at Glen Haven is like that at Dune Park, but on a far grander scale; sometimes there are hollows within it more than 30 meters in depth scooped out by the wind, and reaching down to an ancient beach. Within the dune complex there are extensive old soil lines and many scarred trunks of trees, long buried by the dunes and now resurrected, though not to life.

At many other places along the northern shore of the lake there are high bluffs of clay, or gravel, whose summits are

crowned by established dunes. Only rarely are these dunes in action at the present time, and, where such action is observed, it is clearly due to the rejuvenation of dunes that had become established. The origin of these perched dunes is obscure and hardly within the province of this paper. The formation of dunes at the summit of a bluff is not unknown. A wind laden with sand may sweep up the slopes of a hill. As it reaches the summit its path is no longer narrowly restricted, and as it spreads out, its energy is dissipated and its load deposited. However, no such action was anywhere observed; on the contrary, at many points the wind is removing the dunes from just such locations. Consequently the author rather inclines to the belief that these perched dunes represent an earlier phase of dune formation, when lake or wind conditions were different from the present. Another possible mode of origin will be discussed in connection with the rejuvenated dunes.

The greatest altitude reached by the clay and gravel bluffs is at Empire, a few miles south of Glen Haven; at this point a height of 128 meters is attained. There is a high degree of oscillation in the altitudes even within a few meters. Where the clay bluffs are highest, the perched dunes are seldom as high as where the bluffs are lower. The greatest observed height of the perched dunes above the top of the clay was 60 meters. The greatest total observed height above the lake at Empire was 162 meters; at Frankfort 153 meters. South of Frankfort and north of Glen Haven the altitudes are much less. At Charlevoix and Petoskey there are no cliffs; the dunes are low and superposed directly upon the beach.

The islands in the north end of the lake are of great interest to the student of dunes, since they are exposed to winds from all directions; the position of the dunes thus indicates the direction of the dune-forming winds. In all cases the chief dune formation is on the west coast, and the most conspicuous active dunes are usually restricted to a narrow area at or near the southwest point of each island. Observation from the steamboat revealed the presence of such dunes on South Manitou, South

Fox, and High islands. The dunes on North Manitou and Beaver islands were visited. On North Manitou there are prominent areas of dune activity along the southwest coast, the dunes being superposed on bluffs of clay or gravel. There is a flat-topped terrace here, like that at Glen Haven, but in miniature, the height being only 15 meters and the area scarcely half a hectare; the dune perched on this bluff has been rejuvenated and carried inland a few meters, the greatest altitude being 45 meters above the lake. There are also small wandering dunes superposed directly upon the beach. On the west coast the bluffs are steeper and much higher, at times perhaps 60 meters above the lake; the summits are occasionally crowned by established dunes. On Beaver island the southwest coast was not visited, but there are rejuvenated dunes at various points along the west coast, sometimes 45 meters in height; these dunes are superposed upon the beach. The beach dunes here are exceedingly varied and extensive. As previously stated, there are low beach dunes along the east coast of Beaver island. On Mackinac island there are steep clay bluffs, but no dunes. Thus, the islands plainly show that westerly winds, and especially winds from the southwest, are the chief dune formers.

Surveying the lake region as a whole, the dunes are created and shaped almost entirely by westerly winds. In the southern portions of the lake, the northwest winds have the greater sweep and are the chief dune-formers. Northward the southwest winds are the chief factors in determining the location of dunes. In intermediate localities all westerly winds contribute about equally to dune formation, and there is progressive movement of active dunes to the eastward

III. The ecological factors.

The distribution of the plants in the various dune associations is governed by physical and biotic agencies which will be considered somewhat in detail in another place. At this point it seems advisable to give a general survey of these factors, especially in so far as they affect the distribution of plant societies in the region as a whole.

LIGHT AND HEAT.

Nearly all of the dune societies are characterized by a high degree of exposure to *light*. Particularly is this true of the beach and the active dunes. The intensity of direct illumination is greatly increased by reflection; the glare of the white sand is almost intolerable on a bright summer day. The *temperature* relation is even more marked in its influence upon plant life. Because of the absence of vegetation and the general exposure of sand dunes the temperature is higher in summer and lower in winter than in most localities. This great divergence between the temperature extremes is still further increased by the low specific heat of sand. On sandy slopes protected from cold winds the vegetation renews its activity very early in the spring, because of the strong sunlight and the ease with which the surface layers of sand are heated. Willow shoots half-buried in the sand frequently develop fully a week in advance of similar shoots a few centimeters above the surface. Similarly in the autumn the activity of plant life ceases early largely because of the rapid cooling of the superficial layers of sand, as well as because of direct exposure to the cold.

WIND.

The wind is one of the most potent of all factors in determining the character of the dune vegetation. The winds constantly gather force as they sweep across the lake, and when they reach the shore quantities of sand are frequently picked up and carried on. The force with which this sand is hurled against all obstacles in its path may be realized if one stoops down and faces it. The carving of the dead and living trees which are exposed to these natural sand-blasts is another evidence of their power. Fleshy fungi have been found growing on the windward side of logs and stumps completely petrified, as it were, by sand-blast action; sand grains are imbedded in the soft plant body and as it grows the imbedding is continued, so that finally the structure appears like a mass of sand cemented firmly together by the fungus. The bark of the common osier dogwood is red on the

leeward side, but white to the windward because the colored outer layers of the bark have been wholly worn away. On the windward side of basswood limbs the softer portions are carved away while the tougher fibers remain as a reticulated network. On the leeward side of these same limbs, the outer bark is intact and even covered more or less with lichens.

The indirect action of the wind produces effects that are considerably more far-reaching than any other factor, for it is the wind which is primarily responsible for sand dunes and hence for their floras. But more directly than this, the wind plays a prominent part in modifying the plant societies of the dunes. The wind is the chief destroyer of plant societies. Its methods of destruction are twofold. Single trees or entire groups of plants frequently have the soil blown away from under them, leaving the roots exposed high above the surface; as will be shown later this process is sometimes continued until entire forests are undermined, the débris being strewn about in great abundance. Again, swamps, forests, and even low hills may be buried by the onward advance of a dune impelled by the winds; in place of a diversified landscape there results from this an all but barren waste of sand.

SOIL.

The soil of the dunes is chiefly quartz sand, since quartz is so resistent to the processes of disintegration. The quartz particles are commonly so light colored that the sand as a whole appears whitish; closer examination reveals many grains that are not white, especially those that are colored by iron oxide. With the quartz there are conspicuous grains of black sand, largely hornblende and magnetite. These black grains often accumulate in streaks, persistent for considerable depths and apparently sifted by the wind; large quartz grains are mingled with these grains of magnetite and hornblende so that it would seem as if grains of higher specific gravity are sifted out together with those of greater absolute weight. The sand of the dunes is remarkably uniform in the size of the particles as compared with beach sand; this feature is due to the selective action

of the wind, since the latter agent is unable to pick up and carry for any distance the gravel or large sand particles of the beach.

As is well known, soil made up chiefly of quartz sand has certain marked peculiarities which strongly influence the vegetation. The particles are relatively very large; hence the soil is extremely porous and almost devoid of cohesion between the grains. These features are of especial importance in their effect upon the water and heat relations as shown elsewhere. As a rule, sandy soils are poor in nutrient food materials, nor do they rapidly develop a rich humus soil because of the rapid oxidation of the organic matter.

WATER.

A factor of great importance, here as everywhere, is the water relation. Nothing need be said of atmospheric moisture, since that is sufficient to develop a rich vegetation if properly conserved, as is shown by the luxuriance of neighboring floras. Because of the peculiar physical properties of quartz sand, precipitated water quickly percolates to the water level and becomes unavailable to plants with short roots. The water capacity of sand is also slight, nor is there such pronounced capillarity as is characteristic of many other soils. Again, the evaporation from a sandy surface is commonly quite rapid. All of these features combine to furnish a scanty supply of water to the tenants of sandy soil. The rapid cooling of sand on summer nights may, however, result in a considerable condensation of dew, and thus, in a small way, compensate for the other disadvantages.

The ecological factors thus far mentioned act together harmoniously and produce a striking composite effect upon the vegetation. A flora which is subjected to periods of drought is called a xerophytic flora and its component species have commonly worked out various xerophytic structural adaptations of one sort or another. Again, a flora which is subjected to extreme cold, especially when accompanied by severe winds, takes on various structural adaptations similar to those that are characteristic of alpine and arctic floras. The dune flora is a composite flora, showing both xerophytic and arctic structures. In those

situations which are most exposed to cold winds, one finds the best illustrations of the arctic type, while the desert or xerophilous type is shown in its purest expression on protected inland sandy hills. The discussion of the various arctic and desert structures and their relations to each other will be deferred to the second part of this paper.

OTHER FACTORS.

Certain other factors are of minor importance in determining the character of the dune flora. *Forest fires* occur occasionally, and, as will be shown later, they may considerably shorten the lifetime of a coniferous plant society.

Near cities the vegetation is unfavorably influenced by *smoke* and other products issuing from chimneys. In the neighborhood of the oil refineries at Whiting, Ind., the pine trees especially have been injured or destroyed. A careful study would probably show many plant species that have suffered a similar fate.

The *topography* is often a factor of considerable importance. Dune areas are conspicuous for their diversified topography. This factor determines to a great extent the water relation which has been previously considered, the hills and slopes being of course much drier than the depressions. The topography indirectly affects the soil, since it is mainly in the depressions that humus can rapidly accumulate. The direction of slope is a matter of importance, as will be shown in discussing the oak dunes; the greater exposure of the southern slopes to the sun results in a drier soil and a more xerophytic flora on that side.

Animals do not appear to exert any dominating influences on the dune floras. The dispersal of pollen and fruits by their agency is common here as elsewhere; so, too, the changes that animal activities produce in the soil. Near the cities the influence of man is seen, although such influences are slight unless the sand is removed bodily for railroad grading and other purposes.

The influence of *plants*, which so often becomes the dominant factor, is relatively inconspicuous on the dunes. The most

important function which dune plants perform for other plants is in the contribution of organic food materials to the soil. The oxidation or removal of decaying vegetation is so complete on the newer dunes that the accumulation of humus is not important. On the more established dunes the mold becomes deeper and deeper, and, after the lapse of centuries, the sandy soil beneath may become buried so deeply that a mesophytic flora is able to establish itself where once there lived the tenants of an active dune. The advance of a wandering dune often results in the burial of a large amount of organic matter; when this matter becomes unburied years afterward it may again furnish a soil for plants. Many fossil soil lines have thus been uncovered on the Sleeping Bear dunes at Glen Haven, Mich.

IV. The plant societies.

A plant society is defined as a group of plants living together in a common habitat and subjected to similar life conditions. The term is taken to be the English equivalent of Warming's *Plantesamfund*, translated into the German as *Pflanzenverein*. The term formation, as used by Drude and others, is more comprehensive, in so far as it is not synonymous. It may be well to consider the individual habitat groups in a given locality as plant societies, while all of these groups taken together comprise a formation of that type, thus giving to the word formation a value similar to its familiar geological application. For example, one might refer to particular sedge swamp societies near Chicago, or, on the other hand, to the sedge swamp formation as a whole; by this application formation becomes a term of generic value, plant society of specific value.

Plant societies may be still further subdivided into patches or zones; the former more or less irregular, the latter more or less radially symmetrical. Patches are to be found in any plant society, where one or another constituent becomes locally dominant; zones are conspicuously developed on the beach and in sphagnous swamps. The term patch or zone has a value like that of variety in taxonomy. Authors disagree, here as every-

where, upon the content and values of the terms employed; this disagreement is but an expression of the fact that there are few if any sharp lines in nature. The above, or any other terminology, is largely arbitrary and adopted only as a matter of convenience.

In the following pages an attempt is made to arrange the plant societies in the order of development, the author's belief being that this order more faithfully expresses genetic relationships than any other. In the historical development of a region the primitive plant societies pass rapidly or slowly into others; at first the changes are likely to be rapid, but as the plant assemblage more and more approaches the climax type of the region, the changes become more slow. In the dune region of Lake Michigan the normal primitive formation is the beach; then, in order, the stationary beach dunes, the active or wandering dunes, the arrested or transitional dunes, and the passive or established dunes. The established dunes pass through several stages, finally culminating in a deciduous mesophytic forest, the normal climax type in the lake region. Speaking broadly, the conditions for plant life become less and less severe through all these stages, until there is reached the most genial of all conditions in our climate, that which results in the production of a diversified deciduous forest. On the beach there are to be found the most extreme of all xerophytic adaptations in this latitude, and, as one passes through the above dune series in the order of genetic succession, these xerophytic structures become less and less pronounced, finally culminating in the typical mesophytic structures of a deciduous forest.

A. THE BEACH.

As the author hopes to show in a subsequent paper, the beach formations of Lake Michigan are of two distinct types. One may be called the xerophytic beach, the other the hydrophytic beach. The conditions that determine these two types are not altogether clear, though their distribution suggests some factors which will contribute to the solution of the problem. Dunes are invariably absent from an area occupied by

hydrophytic beaches, partly perhaps because hydrophytic beaches are seldom sandy, and partly because they are commonly found in protected locations. The hydrophytic beaches are found where the gradient of the lake bottom is very slight; as a consequence there is a wide zone of very shallow water in which typical swamp and shallow water plants flourish in great abundance. The bottom is very thickly strewn with gravel and shingle, closely resembling a reef in structure. On the other hand, a xerophytic beach is often sandy, is commonly associated with steep clay bluffs or dunes, and the gradient is much steeper, so that there is a comparatively narrow zone of shallow water. As a consequence, wave action is much more pronounced on the beach proper, as is shown by the great amount of driftwood stranded there. The scanty flora is in striking contrast to the diversified flora of the hydrophytic beach. The greater luxuriance of the flora on the hydrophytic beach is due, in part at least, to the greater freedom from the destructive action of the waves on account of the low gradient. The water supply is also conspicuously greater on the hydrophytic beach, again chiefly because of the low gradient. Inasmuch as dunes are associated only with the xerophytic beach, no further reference will be made to the other beach type.

The xerophytic beach is essentially a product of wave action and comprises the zone which is or has been worked over by the waves. Hence the beach may be defined as the zone between the water level and the topographic form produced by other agents; in the region under study the upper limit of the beach is commonly a fringe of sand dunes or a bluff of clay or gravel. The xerophytic beach in its typical expression is very naturally subdivided into three zones, which may be called the lower beach, middle beach, and upper beach. The lower beach is that zone which is situated between the water level and the line reached by the waves of common summer storms. The middle beach is the second zone, extending up to the line reached by the highest winter storms. The upper beach is essentially a former middle beach which is now beyond the

reach of the waves, and yet is unoccupied by dunes or other topographic forms.

1. *The lower beach.*

The lower beach has been defined as the zone of land washed by the waves of summer storms. It might almost be defined as that portion of the beach which is devoid of vegetation. Perhaps there is no flora in the temperate zone quite so sparse as that of the lower beach, unless we except bare rocks and alkaline deserts. A survey of the life conditions in this zone reveals at once the reason for the scanty vegetation. Land life is excluded because of the frequency and violence of storms; the waves tear away the sand in one spot only to deposit it in another. Even though a seed had the temerity to germinate, the young plant would soon be destroyed by the breakers. Nor is there great likelihood that seeds will find a lodgment in this unstable location. As will be seen later the seeds ripened by tenants of the middle beach are almost entirely scattered away from the lake instead of toward it. The action of both wind and wave tends to carry seeds away from the lower beach. Again, few seeds could endure the alternate extremes of cold and heat, wetting and drying so characteristic of this zone.

Water life is excluded because of the extreme xerophytic conditions which commonly prevail on the lower beach. While algæ may propagate themselves in the shallow pools or even in the wet sand during a prolonged season of wet weather, a cessation of activity if not death itself soon follows the advent of dry weather. During a period of rainy weather in the autumn of 1897 green patches were observed in wet sand a few meters from the mouth of a creek near Porter, Ind. Microscopic observation showed that the green coloration was due to the presence of millions of motile Chlamydomonas forms. These unicellular biciliate algæ were in process of active locomotion in the water held by capillarity between the grains of sand. In all probability these forms migrated to the beach from the waters of the creek during a period of wet weather. It is possible that they might pass into resting stages and live through a season of drought,

were it not for the wind which gathers much of its dune material from the lower beach.

Thus the lower beach is a barren zone between two zones of life. Below it there exist algæ and other hydrophytic forms which flourish in the fury of the breakers; above it there exists the flora of the middle beach, a flora adapted to the most intense xerophytic conditions. At no particular time, perhaps, are the conditions too severe for some type of life; vegetation is excluded because of the alternation of opposite extremes.

2. *The middle beach.*

The middle beach is situated between the upper limits of the summer and winter waves, comparatively dry in summer but washed by the high storms of winter. It may also be defined as the zone of succulent annuals. The upper limit of this beach is commonly marked by a line of driftwood and débris. The instability of the beach conditions is often shown by the presence of a number of such lines, marking wave limits for different seasons. A very heavy storm will carry the débris line far up on the upper beach, to all intents and purposes carrying the middle beach just so much farther inland, as the flora of the next season testifies. Another season may be without the visitation of heavy storms and the middle beach will encroach upon the territory of the lower beach. The limits of the middle beach are altered more permanently by changes in the lower beach. In many places the lower beach is growing outwards, reclaiming land from the lake, while at other points the lake encroaches upon the land. Speaking broadly, the middle beach advances or recedes *pari passu* with the advance or recession of the lower beach. To some extent the débris lines register these changes, as their notable departure from persistent parallelism may indicate; however, there is a considerable lack of parallelism in the débris lines of a single season, owing to variations in the direction of the wind and other factors.

The life conditions in this zone are exceedingly severe, and result in a flora of the most pronounced xerophytic characters.

The fury of the winter storms as they wash over the middle beach, tearing up here and depositing there, excludes almost entirely the possibility of survival through that period. In other words, biennials and perennials are practically excluded from maturing flowers and fruits, although their vegetative structures may flourish for a single season. In the summer the xerophilous conditions are extreme. Nowhere in the dune region are the winds more severe than here; the middle beach is close enough to the lake to feel all the force of its winds and yet far enough away for the wind to pick up sand from the lower beach and bring to bear upon the flora the intense severity of the sand-blast. No flora is more exposed to the extreme desiccating influences of the summer sun than that which grows upon the bare and open beach. Even though the roots can readily penetrate to the water level, the great exposure of the aerial organs to wind and sun results in the working out of that most perfect of all xerophytic organs, the succulent leaf. Just as succulent plants inhabit deserts where no other high grade plants can grow, so, too, they are able to withstand the severe conditions of the beach.

Along the entire eastern shore of the lake, the dominant plant of the middle beach is *Cakile Americana*. At many points this succulent crucifer is almost the only plant species found in this zone, and it is always the chief character species. Two other fleshy annuals are very common tenants of the middle beach: *Corispermum hyssopifolium* and one of the spurges, *Euphorbia polygonifolia*. It is a matter of interest to observe that two of these three character plants of the middle beach, Cakile and Euphorbia, are also characteristic inhabitants of the beach on the Atlantic coast. The significance of the presence of these and other marine forms along the shore of Lake Michigan will be discussed in another place. The above plants are rarely distributed uniformly over the middle beach. The favorite place for growth is along the lines of débris previously referred to; along these lines a greater number of seeds find lodgment than elsewhere, because the waves wash them up from lower levels

and the protection of the driftwood prevents the winds from carrying them on farther. Then, too, the driftwood may furnish some protection to the growing plants, especially protection from winds which might otherwise uproot them. Cakile and Euphorbia reach their culmination on the beach, and when found farther inland it is chiefly on the upper beach or on windward slopes of active dunes. Corispermum, on the other hand, appears to be rather more characteristic of the active dunes than of the beach. Cakile is much the hardiest of the three species, venturing farther out toward the lower beach than either of the other two Of the three, Cakile is the most succulent and perhaps thus best adapted to the extreme xerophilous conditions to which beach plants are subjected. Euphorbia, however, has a copious supply of latex and its prostrate habit would seem to offer some advantages for existence on the beach. Cakile and Corispermum are readily dispersed by the wind, the latter by means of its winged seeds, while the former is a sort of tumbleweed; broken Cakile plants are common sights all over the dunes in the autumn and winter. Corispermum and Euphorbia become less and less common toward the north; at Charlevoix and Petoskey, Cakile is almost the only plant growing on the middle beach, and even this latter species is less common than farther to the south. Thus it seems as though the life conditions on the middle beach are more severe northward than southward, as indeed might be expected.

3. The upper beach.

In the strictest sense the upper beach is not a portion of the beach at all, since it is beyond the reach of the waves; it might perhaps be called a fossil beach, but the fact that it is continuous with the beach proper seems to exclude that term, as does the recency of its fossilization. The expression fossil beach will be reserved for a formation of greater geological age and separated from the present beach by other topographic forms. Where dunes are superposed upon the beach, the upper limits of this third beach zone are quite vague, though the theoretical line of demarcation is where the sand is first accumulated by the wind.

Where clay bluffs are present at the water's edge, the beach is quite narrow and the upper limit fairly well defined, though at times obscured by alluvial fans. Occasionally the upper beach approaches very close to the water's edge; this is the case where the lower and middle beaches are very narrow because of a high gradient. Sometimes the lower or middle beach zone is replaced by a tiny cliff; in such a case the upper beach may approach to the edge of this cliff. The limits of the upper beach, as of other beach zones, are constantly shifting. The lower limits are carried lakeward or landward by the waves of winter storms, but on the whole the lower limits are pushed out more and more lakeward, keeping pace with the advance of the lower beach. The shifting of the wind causes variations in the upper limits, but on the whole the dunes likewise are commonly formed more and more lakeward, as will be shown further on. The three beaches, then, shift from year to year with apparent irregularity, but there appears to be as a resultant a general progressive movement of them all out into the lake. As a whole the three beach zones slope gradually and somewhat evenly upward, toward the dunes or bluffs beyond; depressions, however, are not at all uncommon, and at times they reach down to the water level, so that a beach pool results.

The life conditions are much less severe than on the middle beach, and chiefly because of the freedom from the wave action of the winter storms. The exposure to the sun is almost as great as on the lower zones, but there is more protection from the wind because of the abundance of driftwood. The protective influence exerted by piles of débris is finely shown on the beach at North Manitou island. The upper beach along the south shore of the lake is usually very sandy and comparatively free from driftwood, while the North Manitou beaches are composed chiefly of gravel and shingle with heaps of driftwood piled about in the greatest confusion. The North Manitou flora is one of marked luxuriance, compared with the more southern type, and many mesophytic species are able to get a foothold in the more genial conditions there obtaining. The decay of the

driftwood may also add no inconsiderable portion to the food materials of the beach plants.

The flora of the upper beach is much richer than that of the middle beach, both in species and in individuals, but here as there the vegetation is so sparse that the tone to the landscape is given by the soil. In the region as a whole the most characteristic species of the upper beach are *Artemisia caudata* and *A. Canadensis*.[1]

At nearly all places visited between Chicago and Beaver island Artemisia was present and commonly in abundance. Another plant associated almost everywhere with Artemisia is *Cnicus Pitcheri;* this thistle is seldom so common as Artemisia, but scattered specimens are pretty sure to be discovered on any upper beach. A species scarcely less important in this connection is the beach pea, *Lathyrus maritimus*, another marine plant; locally the beach pea is often the dominant character plant, especially northward. Three other species are character plants over wide areas, as the above three are throughout. *Euphorbia polygonifolia* is a character plant at many stations between Chicago and Glen Haven; its absolute abundance is often as marked on the upper as on the middle beach, though its relative importance is much greater on the latter. *Agropyrum dasystachyum* and *Œnothera biennis* are as characteristic of upper beaches northward as Euphorbia is southward; Agropyrum especially is usually a dominant character plant north of Glen Haven.

None of the above six species are confined to the upper beach. Artemisia is found in most dune societies inland, especially in comparatively naked places. Cnicus is frequent on the dune complex, though less abundant than on the beach, as is also true of Artemisia. Lathyrus appears to be more restricted in its habitat, and in that sense is more typical of the upper beach, though it sometimes occurs on clay bluffs. Euphorbia

[1] Typical forms of both Artemisias have been found, as well as all intermediate gradations, and it is all but hopeless to try to determine which is the more abundant, without careful examination of all the plants in time of fruit. Both species are pubescent in beach and dune habitats, although *A. Canadensis* is the more so.

occurs on the middle beach and also on naked dunes, though less frequently. Agropyrum, though characteristic of northern upper beaches, is still more characteristic of the embryonic dunes. Œnothera occurs on oak dunes and commonly also as a mesophyte.

At this point it will be well to emphasize one of the fundamental principles of ecological plant groupings. It is comparatively seldom that any single species can be regarded as perfectly characteristic of a formation, while a group of five or ten species can be so selected as to enable one to detect that formation almost anywhere within a large area. No one of the above six species can be regarded as perfectly typical of the upper beach, although Lathyrus approaches such a type, but together they form an assemblage that cannot be found in any other formation, except perhaps locally on the closely related beach dunes. Even on these beach dunes, which grade into the upper beach, the relative proportions existing between the above species are very different from those found on the beach, and, as will be shown later, plant species occur on these dunes which are absent from the beach altogether.

Of the six chief character species of the upper beach, three (Œnothera, Artemisia, Cnicus) are commonly biennials, Euphorbia is an annual, while Lathyrus and Agropyrum are perennials with decidedly social habits through extensive rhizome propagation. Thus the perennial habit is much less common on the upper beach than on the dunes. The three biennials pass through the winter in the form of ground rosettes, tall shoots being sent up in the spring. Cnicus has a noteworthy protective covering of woolly hairs.

There are several plant species very characteristic of the embryonic dunes on the beach, which also occur on the upper beach proper, though rarely in great abundance. Notable among these plants are *Ammophila arundinacea*, and *Elymus Canadensis*. Ammophila occurs about equally throughout, while Elymus is much more characteristic northward; indeed on the northern upper beaches Elymus is sometimes as abundant as

Agropyrum or Artemisia. About Chicago Elymus is a common character plant of the dunes, but rarely of the beach. Between Chicago and Muskegon *Asclepias Cornuti* is a frequent tenant of the upper beach. *Calamagrostis longifolia*, one of the chief character plants of the active dunes, is sometimes found on the beach, as are *Solidago humilis Gillmani* (plants large, but leaves not sharply toothed) and *Lithospermum hirtum*, which are more characteristic of rejuvenated dunes, fossil beaches, and heaths. *Cakile Americana* and *Corispermum hyssopifolium* occur but are less abundant than on the middle beach, although the latter is sometimes a prominent upper beach type. The forms discussed in this paragraph are perennials, with the exception of the last two; as they are all of secondary importance, in reality representing the vanguards of a flora which is more at home farther inland, there seems no necessity for any further defense of the idea that the upper beach flora is not typically composed of perennials.

All of the species discussed up to this time are herbs, passing the winter near the surface of the soil or underneath it. The exposure to which shrubs and trees are subjected during the winter is so severe on the upper beach that few of the many dune species have representatives there. The individual shrubs which brave these conditions are relatively scattered, while the plant body is stunted and bears signs of the severe environment provided by the beach. Much the commonest shrub, and the only one which occurs throughout, is *Prunus pumila*, the sand cherry. Poplars occasionally occur, *Populus monilifera* southward and *Populus balsamifera* (both the type and var. *candicans*) northward; so too, the willows, *Salix glaucophylla*, *adenophylla*, and *longifolia*.

The most striking feature of the plant life on the upper beach is the difference in its development at different localities. The luxuriant flora of the north is in marked contrast to the impoverished flora at the south end of the lake. The Dune Park beach, for example, is tenanted only by Artemisia, Cnicus, Corispermum, and a few scattering plants of other species. An upper beach on North Manitou island showed a great abundance of

Elymus, Artemisia, Lathyrus, Œnothera, and *Populus balsamifera*, together with thirty-four other species which were rare to frequent. Among these other species several are of considerable interest: *Anemone multifida*, which also occurs on the beach at Beaver island and on several fossil beaches; *Prenanthes alba*, common in woods and thickets but seemingly out of place on the beach; *Equisetum hyemale*, which grows almost anywhere On similar beaches at Empire, *Achillea Millefolium* and *Equisetum arvense*, two plants which never grow on the beach farther south, are very abundant. *Arabis lyrata* and *Polygonum ramosissimum* (?)[2], the former growing on the inland oak dunes about Chicago, occur on an exposed upper beach at the north end of Beaver island. The reasons for this great luxuriance of the northern upper beaches are not obvious. It has been previously stated that the greater abundance of driftwood on the more northern beaches may furnish considerable protection. This cause seems hardly adequate to account for the great differences, and it may be that climatic or other less apparent factors may have to be called upon. The luxuriance of the northern forests as compared with those about Chicago may need in part a similar explanation.

Interesting beach conditions are to be found on some small islands that have recently formed on reefs in the vicinity of Beaver island. During the winter and spring blocks of ice laden with stones are stranded on these reefs; thus they are gradually built up to the lake level. Wave action comminutes the reef materials forming a soil suitable for plant life; the waves and winds also constantly add to the area of the islands. One such island is about 200 meters in length, five or ten meters in width, and scarcely thirty centimeters high. The flora of this unprotected island is a swamp flora, *i. e.*, the island is in its entirety a hydrophytic beach. Another island, somewhat larger and considerably older, has an altitude of one or two meters at its highest point. The beach toward the southeast, east, and northeast is hydrophytic, while that toward the northwest, west, and southwest is xerophytic. Undoubtedly the degree of exposure to the

[2] A remarkable dwarf Polygonum with six stamens, very different from the type.

wind is the chief cause which determines the nature of the flora on this island. Not only is the wind more severe on the west beach, but the waves pile up more sand on that side of the island and hence produce a drier soil. The flora on this xerophytic upper beach is remarkably complete and diversified, showing a distinct zonal distribution. Above the middle beach there is a zone characterized by the dominance of *Elymus Canadensis*, then a zone of *Geranium Robertianum*, then a zone of *Artemisia Canadensis*, and finally a zone in which *Cornus stolonifera* (or *C. Baileyi* into which it grades) is the chief character plant. Scattered more or less with these are *Prunus pumila*, *Œnothera biennis*, *Lathyrus maritimus*, *Cnicus Pitcheri*, *Agropyrum dasystachyum*, and *Populus balsamifera*. *Pastinaca sativa* and *Geranium Robertianum* are common here, and are remarkable inhabitants of a xerophytic beach, since both are usually inland mesophytes. Two other plants occur on this beach that are south of their chief range and rare in the Lake Michigan region, *Tanacetum Huronense* and *Anemone multifida*. The flora of this isolated island beach is remarkably prolific; scarcely a single upper beach type is absent. It is obvious that the means of plant dispersal are so uniformly successful, that almost an entire flora may be transported to a newly formed island within a few years.

One other common feature of upper beaches should be mentioned. As noted above, there are irregularities in the slope of the beach often resulting in depressions which reach below the water level. Such depressions may be called beach pools and of course have a hydrophytic flora; this flora, however, is not the flora of a hydrophytic beach. Beach pools are relatively protected from the action of winds and waves; the chief difference from a hydrophytic beach is that the latter is washed by the fresh waters of the lake, while the beach pools are far less constantly supplied with fresh water. The conditions in the latter approach somewhat those of the ill-drained inland sloughs between the sandy ridges. By far the most characteristic plant about the pool margins is *Juncus Balticus littoralis;* this species is more xerophytic than most of its genus, and often creeps well up on

the xerophytic upper beach. *Triglochin maritima*, *Potentilla Anserina* and several species of Salix also occur about the margins of the pools.

4. *Fossil beaches.*

In regions where dunes are superposed upon the beach, portions of the beach may remain unoccupied by the wind-blown sand, appearing as islands in a sea of dunes. Or a beach which has been covered by the dune-complex may later be uncovered, exposing the gravel and shingle of an ancient shore. In any case these ancient or fossil beaches, separated as they are from the present beach by dunes, are more highly protected from the wind than the beaches which have been previously described. The cold winds lose little of their energy while sweeping up the gradual slopes of an ordinary beach, but their force is considerably broken by a line of dunes. Fossil beaches which have been uncovered by the dune complex occur at Dune Park, but to such a limited extent that a typical flora is not developed The most extensive fossil beach observed was at Glen Haven, where an area several hectares in extent has been denuded of its covering of sand to help supply the extensive dune complex. Similar but smaller fossil beaches were seen at Saugatuck and North Manitou island. Associated with the fossil beach is a formation which may not represent a beach at all. In the general description of the region, reference was made to the high terrace-like bluffs along the northern portions of the lake shore. These miniature plateaux, from which former sand dunes have doubtless been removed, exhibit a surface of gravel, which produces the appearance of a fossil or a true beach. The most extensive of these flat gravel-topped hills are at Glen Haven; similar but less extensive formations of this type were seen at Frankfort and North Manitou island.

The floras of the fossil beaches and the gravel terraces 120 meters above the present beach are essentially identical, although the latter apparently have a greater exposure. Both the beaches and terraces have a flora which resembles that of the upper beach in a general way, but there is a pronounced decrease of most of

the typical beach forms and a pronounced increase of the more inland types. Thus the flora clearly illustrates the greater protection from exposure which is enjoyed on the fossil beach. The Artemisias are as characteristic of the fossil beaches and terraces as of the upper beach, but none of their five chief beach associates retain their prominence here. *Cnicus Pitcheri* occurs frequently, but chiefly at the lower level; *Euphorbia polygonifolia* and *Œnothera biennis* were observed but rarely and only at the lower level; Lathyrus, Corispermum, and Agropyrum were not found at all. In place of these upper beach plants the Artemisias have a new crowd of associates. In general the terraces and fossil beaches have four dominant character plants, *Artemisia Canadensis* (or *A. caudata*) as already named, *Solidago humilis Gillmani*, *Lithospermum hirtum* and *Andropogon scoparius*. Solidago and Lithospermum were noted as occurring at times on the upper beach, but they are far more common here. Andropogon was not observed on the true beach, but is very common on fossil beaches and terraces, its scattered bunches or tufts forming one of the chief landscape features.

On the more northern fossil beaches several species are almost as characteristic as those named in the preceding paragraph. Prominent among these forms are *Zygadenus elegans*, *Campanula rotundifolia arctica*, and *Arenaria Michauxii;* northward these types are almost wholly confined to the fossil beaches or terraces, although Zygadenus is sometimes present on the upper beach. *Anemone multifida*, *Kœleria cristata* (*?*) and *Arabis lyrata* occur northward but are less frequent. A very interesting plant which sometimes frequents fossil beaches is *Hudsonia tomentosa*, a species noted for its habit of forming scattered clumps of densely tufted growths. Other occasional tenants of the terraces and fossil beaches are *Populus monilifera*, *Prunus pumila*, *Calamagrostis longifolia*, and *Solidago nemoralis*.

While the fossil beach looks backward to a true beach history, it commonly looks forward to a heath. Largely protected from the accumulation of sand, they furnish a situation favorable for the development of a juniper-bearberry heath. Such heaths are

in process of formation at Manistee, North Manitou and elsewhere, and will be described in another place.

B. THE EMBRYONIC OR STATIONARY BEACH DUNES.

1. *Dunes of rapid growth (primary embryonic dunes).*

Many of the lake winds which blow across the beach have a surplus of energy, and are able to select out the finer grains of sand and carry them farther from the shore. The action of the wind in transportation is analogous to that of water. The finer particles are picked up bodily by the air currents, while the larger particles are blown or rolled along on the beach. Whenever an obstacle is met, some or all of the load is necessarily deposited by the wind. The coarser particles are deposited upon or about the obstacle, while the finer particles form a diminishing trail on the lee side. As soon as the deposition is sufficient to relieve the overladen wind, the trailing of sand ceases, and the wind continues with its lessened load until another obstacle is reached. So long as the wind blows continuously from one direction, the mound of sand keeps growing and the trail to the leeward becomes more and more conspicuous. Indeed, the growth increment is often greater during the later stages of a continuous wind current, since the growing mound of sand becomes more and more an obstacle to the progress of the laden wind. As a result of this action, there appears a topographic form with a steep windward side and a gently sloping leeward side.

When the wind changes, the trails of sand are no longer in the lee of the obstacle, but are more or less exposed to the wind, and hence are rapidly removed. The contour of the mound is changed and there results, just as before, a topographic form, steep to the windward but gently sloping to the leeward. It will thus be seen that it is always possible in dry weather to determine the direction of the last strong wind by observing the position and direction of the leeward trails of sand. A clump of grass with a poorly developed leeward trail may be seen in the foreground of *fig. 4*.

Under ordinary conditions no permanent results follow from such wind action as has been described, since one wind destroys the products of another. There is, perhaps, a tendency for sand to accumulate on the landward side of obstacles, since the energy of the lake winds is likely to be greater than the energy of winds from other directions. But no extensive dune formation can occur on the beach, unless the obstacle, which compels the wind to deposit its load, is itself increasing in size. A mound of sand, which is being built up by the wind, becomes more and more a formidable obstacle to the progress of the sand-laden currents, and it might be supposed that the growth of such a mound would continue indefinitely. Such does not appear to be the case on the beaches studied. The wind blows over the beach from so many directions and with such resistless energy that mounds of sand rarely accumulate without the aid of other factors.

The formation of beach dunes, then, depends upon something more than wind and sand. An obstacle is needed which will grow *pari passu* with the dune, and such an obstacle is furnished by a number of perennial plants, which spread by means of rhizome propagation. These dune-forming plants must be perennials; otherwise the dune would be destroyed at the end of the growing season. Such annual dunes are very common on the beach. Clumps of Cakile have been seen, about which there is piled a miniature dune. In the same manner there may be formed biennial dunes about individual plants of Artemisia or Cnicus. A perennial dune, however, requires perennial dune-formers. A second necessity in a dune-former is the ability to spread radially by rhizome propagation, for only in this way can the area of the obstacle and the area of the dune be enlarged. The only notable exception to this rule is found in the case of cottonwoods and such perennial grasses as Andropogon and Elymus; these plants grow in groups or tufts and will be described later.

The plant which serves as an obstacle for the wind must also possess the power of growing out into the light when buried by

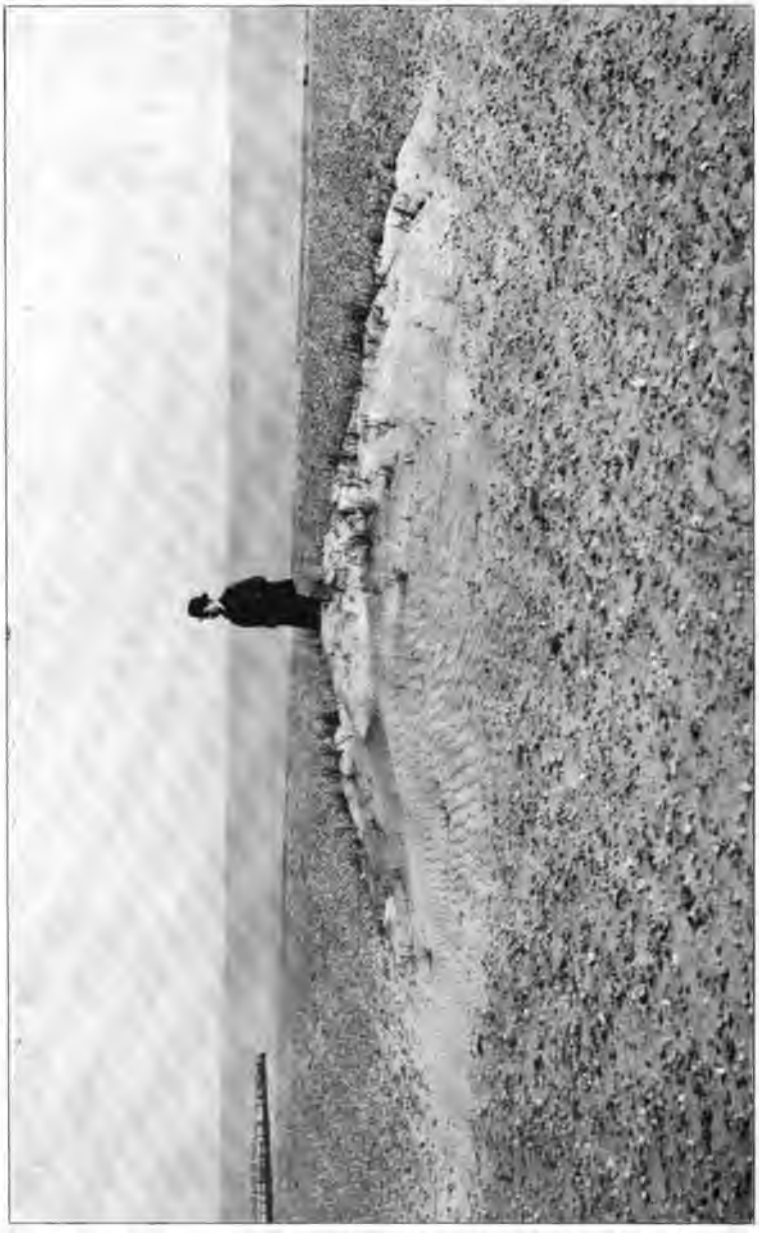

FIG. 2.—Embryonic dune on the beach at South Chicago, formed by the sand reed, *Ammophila arundinacea*. Leeward trail of sand at the left.

FIG. 3.—Embryonic Ammophila dune on the beach at South Chicago, some years older than that shown in *fig. 2*. Sinuous trough at the center, where there is no vegetation.

the sand. This property permits the rise of the dune in altitude, as rhizome propagation permits the increase in area. Most plants are excluded by reason of this third requirement, partly because they are unable to rise above the sand when buried, and partly because stem elongation increases the difficulty of drawing up a sufficient supply of water from the soil. The roots of dune plants are often uncovered and exposed to wind and sand-blast action; hence plants unable to survive a period of root exposure cannot live in such a habitat. In short, a successful dune-former must be able at any moment to adapt its stem to a root environment or its root to a stem environment. The vicissitudes of existence on an embryonic dune are greater than anywhere else, except at a few points on the dune-complex. In addition to the above particular requirements, a dune-former must, of course, be perfectly equipped with a set of the most extreme xerophytic adaptations. Nowhere else except on the beach is there so great exposure to heat, cold, and wind.

The most typical and successful of all dune-forming plants along Lake Michigan is the sand reed, *Ammophila arundinacea*. The life history of an Ammophila dune will now be given, and may be taken as the average life history of a stationary beach dune. Whenever a tuft of this or any similar grass gets a foothold on the upper beach, the sand drifts along and is lodged in between the stems and leaves, as already described (see foreground, *fig. 4*). The leeward trail of sand changes its position as the wind varies its direction, but the sand deposited between and around the blades of grass is not easily dislodged. The radial propagation of the tuft of grass causes an areal extension of the miniature dune. So, too, there is an increase in altitude, since the grass constantly grows higher in its endeavor to lift itself above the sand. This upward growth enables more sand to accumulate; in other words, the grass and the dune grow *pari passu* outwards and upwards. The result of several years of this symbiotic growth of dune and grass may be seen in *fig. 2*, which represents a small embryonic dune on the beach at South Chicago, Ill. The general contour of the dune is seen to be

FIG. 4.—Embryonic dunes on the South Chicago beach. Tuft of grass in the foreground just beginning to collect sand, also with a leeward trail. Dune at the center formed by many tufts of Elymus acting together.

determined by the Ammophila; toward the left is the leeward trail of sand left by the last wind. *Fig. 3* represents an older and larger Ammophila dune on the same beach, viewed from the lakeward side and hence not showing any leeward trail of sand. Not only is the general contour of this dune determined by the Ammophila, but there will be observed a somewhat sinuous trough toward the center, where there happens to be no vegetation. This shows how readily the dune would be removed were it not for the plant life present. Thus Ammophila is not only an efficient dune-former but also a dune-holder.

While Ammophila is the most common dune-former and perhaps the best adapted for that difficult task of all our lake shore plants, many other species play a similar rôle. On the northern beaches *Agropyrum dasystachyum* is very common as a dune-former; its habit is exactly that of Ammophila, and consequently needs no description. *Elymus Canadensis* and *Calamagrostis longifolia* may be regarded as dune-formers, but they are of less importance than Ammophila and Agropyrum. A typical Elymus dune, as found on the South Chicago upper beach, is represented at the center of *fig. 4*. These grasses grow in tufts and do not have any extensive vegetative propagation, but the tufts may be so close together as to act like a large social clump of Ammophila.

Certain shrubs are of almost equal importance as dune-builders with the grasses. Among these, the willows, *Salix adenophylla* and *S. glaucophylla*, and the sand cherry, *Prunus pumila*, deserve especial mention. All of these shrubs have social habits, and rapidly increase their area of control in all directions. The willows are particularly well fitted to build up a perennial beach dune. They are about as well adapted to a xerophytic environment as are any of the grasses, and their vegetative increase is about as rapid. The fact that they are shrubs and have a greater power of vertical stem elongation makes them even better fitted to rise above the sand. When a shoot of one of these willows is buried, roots are sent out from all the buried portions, even up as far as the floral axis. The willows, too, can

FIG. 5.—Embryonic dune at Dune Park, formed by the cottonwood, *Populus monilifera;* viewed from the leeward side. Trees partially buried. Steepness of slope shown by the streaking of the sand. Tendency of vegetation to creep up the lee slope.

be uncovered without suffering serious injury. In short, the species of Salix are able to adapt their stems to a root environment, or *vice versa*, better than any other plants found along the coast. Hence the willows stand abreast of Ammophila as dune-formers. Another shrub that seems to have all the necessary requirements for a dune-builder is *Cornus stolonifera* (or *C. Baileyi*), though it is probably less fitted for a xerophytic life; however, Cornus dunes are by no means rare on the beach.

The only trees which make any significant contribution to dune formation are the poplars, *Populus monilifera* and *P. balsamifera*. Of these, the former is the more important, especially southward. These trees have little or no vegetative propagation of the willow type. Every year great numbers of cottonwood seeds germinate in protected depressions on the upper beach. As the young plants grow rapidly, it is not long before they form groups dense enough to retard the sand-laden winds. Thus a cottonwood dune is formed, a type which characterizes the Lake Michigan shore at very many places. A cottonwood dune a number of years old is shown in *fig. 5*. It is possible to see, even from the photograph, that the lower portions of the trees are covered by the sand. The growth of a cottonwood dune, therefore, is of a symbiotic nature, exactly as is the growth of an Ammophila dune, in spite of the great difference between the life habits of these two dune-formers.

The controlling part which plants play in dune formation is still further shown by the variations among the embryonic dunes as to area, shape, and height. Dunes that are formed by Agropyrum, Ammophila, or Salix are capable of indefinite areal expansion, since these plant types have extensive vegetative propagation. Populus or Elymus dunes, on the other hand, always retain essentially the same area, since there is little or no vegetative reproduction, and since the opportunity for any further development of seedlings is removed. Young seedlings are often found in the moist sand of the depressions, but never in the dry sand of the dunes. The Agropyrum dunes are always very low, seldom if ever a meter in altitude. The Ammophila dunes are

higher because this latter plant type has a greater power of upward growth than has the former. Both the Agropyrum and Ammophila dunes are alike in being relatively large and low, with slopes almost as gentle as those of the beach. The Salix dunes are equally large, but higher and steeper because of the greater power of upward growth. The Prunus dunes are very small because of the slight vegetative propagation, and yet they are relatively high and steep because of the pronounced power of upward growth.

The cottonwood dunes are the highest of all, often having an altitude of several meters, because the cottonwoods grow higher than any other dune-former; they are also the steepest because there is no vegetative propagation. The steep slope of a cottonwood dune is shown in *fig. 5;* the marks in the sand at the right are the paths made by the movement of the sand down the steep slope, and indicate a gradient of about 30°. *Figs. 2* and *3* indicate the gentle slope of the Ammophila dunes. The cottonwood dunes are commonly long ridges parallel to the lake shore. This is partly due to the fact that the depressions in which the seeds germinate are parallel to the shore, because of wave action. The prevalence of lake winds perpendicular to these ridges also helps these topographic forms to retain their original shape. Summing up this matter, then, the area of a beach dune is determined chiefly by the amount of the vegetative propagation of its tenants, the steepness is determined by the rapidity of this propagation, and the altitude by the power of the dune plants to increase in height.

Of the dune-forming species, *Ammophila arundinacea* and *Salix adenophylla* are the most abundant, occurring almost everywhere that beach dunes exist. These two species are most at home when half-buried in the wind-blown sand, and occur much less frequently in other associations. *Prunus pumila* and *Calamagrostis longifolia* occur throughout the region, but are less characteristic of the beach dunes than are the first-named species. Prunus is common on the upper beach, as already shown, and also on the heath; Calamagrostis is particularly characteristic of

the larger active dunes. *Agropyrum dasystachyum* is very common at Glen Haven and farther north, and, like Ammophila, is most at home on the beach dunes. *Populus monilifera* is very common south of Glen Haven; the cottonwood dunes are usually formed farther inland than the other types. This species is replaced northward to some extent by *Populus balsamifera* and its variety *candicans* (both sometimes on the same tree!), though this poplar is much less of a dune-former than the cottonwood. *Salix glaucophylla* is frequent on the beach dunes, especially southward, but is more characteristic of the swamps; the same may be said of *Cornus stolonifera*. *Elymus Canadensis* is not abundant anywhere on the beach dunes.

An interesting corollary may be deduced from the last three paragraphs. Since various dune forms are caused by differences in the life habits of the dune-forming species, it follows that the distribution of certain topographic forms coincides with the distribution of the dune-formers. Low dunes of the Agropyrum type are not found at the south end of the lake. The steep ridgelike cottonwood dunes are common southward, but rarer northward, since cottonwoods are rarer northward. This is only one of the many cases where ecology helps to interpret physiography.

The dune-forming plants are not the only tenants of the beach dunes. Most of the species that grow on the upper beach are also frequently present on the dunes. Those of especial importance are *Artemisia Canadensis* (or *A. caudata*), *Cnicus Pitcheri*, *Lathyrus maritimus*, *Euphorbia polygonifolia*, and *Corispermum hyssopifolium*. By reason of its extensive vegetative propagation, *Juncus Balticus littoralis* sometimes serves as an obstacle to sand-laden winds, and by a limited subsequent growth results in the formation of miniature dunes. *Lithospermum hirtum*, though more characteristic of embryonic heaths and rejuvenated dunes, sometimes ventures out upon the beach dunes. It should be likewise noted that any of the dune-forming species are likely to grow on dunes that are formed in the main by others, although the vegetation of individual embryonic dunes is often composed of a single species.

Though no plant formation anywhere can have a much larger percentage of plants that are entirely independent of other plants, the beach dunes, nevertheless, have occasional forms that are parasitic, saprophytic, or epiphytic. Various unidentified Basidiomycetes have been found in the most open places, deriving their nutriment from buried driftwood. The most notable parasite found was *Aphyllon fasciculatum*, a plant which derives its nutriment through attachment to the roots of Artemisia. Lichens are abundant on the cottonwoods at all places that are not directly exposed to a fierce sand-blast action. Common lichen species in such places are *Physcia stellaris*, *Theloschistes concolor*, and *Placodium sp.*

Interesting beach dunes were seen on the shores of two small inland lakes, Crystal lake, near Frankfort, and Fount lake, on Beaver island. In each case the lakes approach a dune area near the shore of Lake Michigan, suggesting the probable origin of the sand; there can be no question, however, but that the sand composing these beach dunes was washed up by the waves of the small inland lakes and worked over by the winds, exactly as described in the preceding pages. The dune-forming winds at Crystal lake are easterly winds, chiefly because the source of sand is on the west side of the lake, and it is on the west shore that the dunes are located. There are typical Ammophila dunes at this point. Among the other plants growing here are Artemisia, Cnicus, Populus, Cornus, Prunus, Lathyrus, Œnothera, Corispermum, Calamagrostis, Elymus, and Juncus. At no place on Lake Michigan was a more typical and varied beach and beach dune flora observed than on the west shore of Crystal lake.

2. *Dunes of slow growth* (*secondary embryonic dunes*).

Dune formation is by no means confined to the upper beach, but may take place anywhere that the sand is able to collect, provided the plants at that place are fitted to be dune-formers. The formation of dunes on the dune-complex and on rejuvenated dunes is essentially like that on the upper beach, and will be discussed later. New dunes of a very interesting type are in

process of formation on many fossil beaches and on the gravel terraces. As has been previously stated, the terraces and fossil beaches are better protected from the wind than is the upper beach, and there is in consequence not only a more luxuriant flora, but also a different plant assemblage. The sand which blows across these places, though less in quantity and less furiously driven, nevertheless is capable of dune formation if the proper plant species are present. Several of the beach dune-formers also occur on the terraces and fossil beaches, and build up small dunes. Among these are Ammophila, Calamagrostis, Prunus, and Populus.

Among the dune-formers on terraces and protected fossil beaches, one of the most interesting is *Andropogon scoparius*. This grass grows in tufts and is very abundant, as has been already stated. About each tuft a mound of sand has often collected. A photograph showing the striking appearance of an area of Andropogon dunes was unfortunately spoiled, but its appearance is much like that of an area of *roches moutonnées*, as figured in geological works. Hundreds and sometimes thousands of these miniature dunes may be seen in a single landscape. *Arctostaphylos Uva-ursi* and *Juniperus Sabina procumbens* are dune-formers within moderate limits. Both of these shrubs are procumbent creepers, and hence unable to rise above the sand to any considerable height, probably never as much as a meter above their original position. It is for this reason that such hardy plants as these cannot grow successfully on an upper beach that is exposed to extensive sand drifting. The above three species are the most prominent dune-formers in protected places. Arctostaphylos dunes occur throughout, and are not confined to fossil beaches, but are also common on exposed heaths. The Andropogon dunes were not seen except on fossil beaches, although this grass is common along the entire coast. The Juniperus dunes occur chiefly northward.

The dune formation seen on east coasts was chiefly of this small, slow-growing, secondary type. The dunes at Waukegan, in part at least, are formed by Juniperus. On the east shore of

Beaver and North Manitou islands, there are a number of low dunes formed conjointly by Juniperus and Arctostaphylos. There are low slow-growing Juniperus dunes on the shore of Fount lake on Beaver island; in addition to the procumbent juniper, *Juniperus communis* and *Gaylussacia resinosa* assist in dune building here. The Andropogon dunes are better developed on the fossil beaches of North Manitou island than at any other point visited. On these same fossil beaches, *Hudsonia tomentosa* serves in a small degree to collect the wind-blown sand. On the east shore of North Manitou island, the pasture grass, *Poa compressa*, forms miniature dunes.

Near the beach at South Chicago there are swampy depressions tenanted by *Potentilla Anserina* and *Polygonum Hartwrightii*, plants which are best developed in low grounds but which often creep up to higher levels. On these higher levels near the beach they collect the drifting sand and are able to form low dunes, similar to Arctostaphylos. These plants show a most surprising plasticity, since a single individual developed in a swamp is able to adapt itself to a mild type of dune existence. Another swamp plant, *Cephalanthus occidentalis*, occurs near the same beach and in a similar way helps to build these low slow-growing dunes. The conversion of swamp plants to dune plants will be discussed more at length in another place.

The most extensive area of dune formation on the beach was seen on the west shore of Beaver island. *Fig. 6* shows a small portion of this area. This place is of peculiar interest because there is a perfect series of gradations between the rapidly growing dunes first described and those of the slower growing type. Toward the beach proper (foreground, *fig. 6*) there are dunes formed by Salix, Prunus, and other high-grade dune-builders. Farther back, toward the taller and older dunes of a previous epoch, there may be seen low dunes built by Arctostaphylos, Juniperus, and *Potentilla fruticosa*, small dune excrescences on a general dune substratum. The life-history of these dunes appears to have been as follows. First a stage of dune formation by such plants as Salix, then, as vegetative propagation

allowed these plants to encroach more and more lakeward upon the broad beach, new dunes were formed nearer and nearer the lake. Or, perhaps, there was a recession of the lake and a consequent extension of the beach into new territory; these new dunes may have thus been formed farther and farther lakeward, keeping pace with the advancing shore line. In any event, the interposition of a new row of dunes between the lake and

FIG. 6.—Embryonic beach dunes at Beaver island. Primary Prunus and Salix dunes in the foreground. Secondary Arctostaphylos dunes superposed on primary dunes, at the center of the picture. Old lines of established coniferous dunes in the background, becoming rejuvenated at several points.

those first formed essentially changed the life conditions on the latter. The row of dunes nearest the lake serves as a windbreak. The first row catches most of the drifting sand, and the second catches most of what remains. This fact makes it possible for the slow dune-formers to inhabit the more inland of the ridges. Expressed in other words, the high-grade or primary embryonic

dunes encroach upon the lake, not by the actual advance of an individual dune in that direction, but by the formation of new ones; in like manner the low-grade or secondary embryonic dunes encroach upon the former type, using the topographic form of the primary dune as a base of operations, and building new dunes as low excrescences upon the old.

The advance of a dune area toward the lake, as just described, shows how the coastal belt of dunes may grow wider as the years pass by. In another place it will be shown how they may also grow wider by the actual advance of an individual dune upon the land. In concluding the section on the embryonic dunes, it may be well to emphasize in another way the radical difference between the two types that have been discussed. Their intimate gradation, as shown at Beaver island, is by no means the universal fact. Perhaps it is even more common for one of the primary type to leave its original habitat and wander across the country as an active dune. The secondary type never has that history; an Arctostaphylos dune almost always grows into a heath.

C. THE ACTIVE OR WANDERING DUNES. THE DUNE-COMPLEX.

1. *Transformation of stationary into wandering dunes.*

The symbiotic growth of the beach dunes and their builders may go on for years, but a prolonged existence of these relations is unlikely. As the mounds get larger and higher the conditions for further accumulation of sand become, if anything, more favorable. It is not so with the plant tenants, for each year they are raised farther from their chief base of supplies, the water level. It is probable, also, that the desiccating influence of radiant energy and wind upon the aerial organs becomes greater and greater as the years go on, because of greater exposure at the higher levels. Again, the dune-formers, although perennials, do not have an indefinite duration. The life cycle of the cottonwood is relatively short for a tree. All of the other prominent dune-formers spread more or less by vegetative propagation, so that it is difficult to determine a definite life cycle.

Even though an existence of indefinite duration might be secured through vegetative propagation, many individual shoots must die in the course of time.

In one way or another, then, dune formation ceases and another phase of dune history begins. There is here an end of the stationary beach dunes, a beginning of the wandering dunes. When the plants are no longer able to oppose its progress, the first effect of the untrammeled action of the wind is seen in a tendency to reshape the topographic forms. The beach dunes heretofore described are more or less symmetrical, because of the tendency toward symmetrical plant growth. A dune fashioned entirely by the winds without the assistance of plants is never symmetrical. The windward slope has a very gentle gradient, usually about 5°, and because of the destructive action of the wind, this slope is topographically rough and uneven. The leeward slope, however, is much steeper, averaging about 30°, and is very smooth and even, because determined by gravity instead of wind. The wind sweeps up the gentle windward slopes, blowing or rolling the sand along until the crest is reached; here the sand is deposited by the wind and it rolls down the steep slope, spreading itself quite evenly. *Fig. 17* shows an average gentle windward slope, *figs. 13–15* steep leeward slopes.

The Prunus dunes are particularly favorable for a study of the origin of an active dune, since their form is most at variance with that of the wind-shaped dune, as described above. A Prunus dune is commonly a low cone more or less rounded at the top. As soon as the plants are dead, and sometimes long before that event occurs, the wind endeavors to reduce the windward gradient by removing the sand toward the top and blowing it over on the other side. In this way the roots are exposed and existence made less endurable, if the plant is still living. Prunus dunes with roots exposed on the windward side are common at Dune Park, Beaver island, and elsewhere. On the terrace at Glen Haven, some dunes have been carried beyond their former resting place, leaving the scraggy clumps of Prunus roots at the rear.

What has been said of the Prunus dunes holds more or less for the other types. The cottonwood dunes especially are peculiarly subject to the destructive attacks of the wind, since their shape also notably fails to correspond with that of a normal wind-made topographic form. The lower Ammophila, Salix, and Agropyrum dunes are less likely to suffer destruction, and yet small Ammophila dunes were seen on the dune-complex at Glen Haven that had been blown away from their first abode, leaving the Ammophila stranded at the rear. Even while living, these dune-formers were unable to hold the dunes which they had helped the wind to build; much more when dead are they likely to have the dune swept on beyond them.

The destructive action of the wind and the transformation of a stationary into an active dune are very much retarded by the tenacity with which the stems and roots retain their place, even when dead. A plant which thus has the power to hold its position and keep the sand from being blown away is commonly called a sand-binder. In this connection it may also be called a dune-holder, as it has been already called a dune-former. Perhaps the most tenacious of all the dune-holders on the coast of Lake Michigan is *Calamagrostis longifolia*. This grass, as has been seen, is not of first importance as a dune-builder, but when it has once built up a dune it seems almost impossible to dislodge it. At the left of the basswood tree in *fig. 23*, there is shown a clump of Calamagrostis directly facing the prevailing wind at the summit of a mound, and stubbornly holding its position. The leaves, stems, and roots are all stiff and wiry, almost perfectly resisting the mechanical action of the wind. The roots in the sand form a network so dense that it is almost impossible for the wind to remove the sand from among them.

From an economic standpoint, *Ammophila arundinacea* is a more successful dune-holder than is Calamagrostis, but its greater success is due to its extensive vegetative propagation. The dense social growths of Ammophila make it difficult for the wind to get a start in the process of sand removal, whereas the sand can be readily picked up from between the more scattered

tufts of Calamagrostis. An individual tuft of the latter, however, seems to be much more resistant than a tuft of Ammophila. Calamagrostis, too, grows in more exposed situations than does the other grass, and hence is a valuable dune-holder in places where Ammophila might not thrive at all.

Another noteworthy dune-holder is *Prunus pumila*. A very common sight on the upper beach is a truncated cone literally covered at the summit and sometimes on the sides with a dense tangle of dead stems and roots of the sand cherry. The wind has removed all the sand which it can reach and is obliged to wait until the stems and roots decay sufficiently to allow the wind to blow them away and get at the sand beneath. Prunus is one of the first plants to succumb before the dune in the process of dune formation; perhaps its life cycle is normally short, but more probably the process of drawing up water a greater and greater distance each year compels the plant to give up the unequal struggle.

Sooner or later the dead roots and stems of the dune-holders are all removed, and the wind becomes the undisputed master of the situation. If there is a sufficient amount of sand still remaining, the once stationary dune begins to move, not bodily, of course, but none the less steadily and surely. The sand is swept up the low gradient of the windward side, deposited at the crest, and carried down the steep leeward slope by gravitation. In this manner successive parallel layers of the windward slope are carried over the crest, and the dune as a whole advances inland. The simple life-history just outlined is the exception, not the rule. Much more commonly the sand is scattered in many directions, collecting wherever new lodging places can be found. These processes of deposition and removal, dune formation and dune destruction, are constantly going on with seeming lawlessness. However, in the district as a whole the sand is constantly increasing in quantity, whatever may be true of the individual dunes here and there. The outcome is certain to be a wandering dune in the process of time, unless the actions of the wind and wave are checked. Because of the complexity of the

conditions when the movement across the country becomes a conspicuous fact, it seems well to apply the term dune-complex to the totality of topographic forms which make up the moving landscape as a whole.

2. *Physical and biological features of the dune-complex.*

It will not be necessary to trace farther the changes involved in the transformation of simple beach dunes into a dune-complex, although the coast of Lake Michigan shows all of the intervening stages. Inasmuch as a single dune-complex illustrates almost all conceivable conditions of a dune's life-history, a careful description of a typical dune-complex will involve all of the essential points. The dune-complex is best developed at Glen Haven, Mich., and Dune Park, Ind. All of the essential features are present in both areas, though developed on a grander scale at Glen Haven. The Dune Park area has been most carefully studied, and most of my photographs were taken there.

The dune-complex is a restless maze. It is a maze because all things that a dune ever does are accomplished there. While there is a general advance of the complex as a whole in the direction of the prevailing winds, individual portions are advancing in all directions in which winds ever blow. It is not at all uncommon to find small dunes advancing over the dune-complex back toward the lake. At Dune Park the main line of advance is southeast, yet some small dunes advance toward the northwest, because taller dunes are situated between them and the lake. These little dunes in the lee of large ones are protected from the westerly and northerly winds but feel the full force of the easterly and southerly winds, and hence advance contrary to the prevailing direction. It is thus a common sight to see two dunes advancing to meet each other; when they come together, of course the two dunes become one and move in the direction of the prevailing winds. From this account it is easy to see that small dunes on the complex may advance in any direction, provided only that they are protected from winds blowing in other directions.

The dune-complex, however, is much more than a maze of little dunes wandering in all directions. At many points there are to be found the stationary embryonic dunes that have been previously described. All stages of their life-history may be seen; the beginning, the climax, the destruction. Here and there the wind sweeps out great hollows, which reach down almost to the water level. Great troughs are carved out by the

FIG. 7.—Trough-shaped wind-sweep at Beaver island. Dead roots and branches of plants that have been torn up. Embryonic dunes in the background formed of sand brought from the foreground. Sparse annual vegetation in the wind-sweep.

wind, chiefly at right angles to the lake, but also at all other angles. Here and there vegetation has obtained a foothold on the complex, thus converting portions of it into an established dune. These established dunes may become rejuvenated, or the vegetation may spread until it covers large portions of the complex. The most striking feature of the dune-complex, then, is its topographic diversity.

To one who visits a dune-complex season after season, another feature comes to be as striking as its diversity, and that is its restlessness. From a distance the complex seems always the same, a barren scene of monotony, but the details are never twice alike. A little dune arising on the complex has become enlarged, another has passed from existence without leaving a trace behind. Where a dune was advancing last year, there is now, perhaps, a hollow swept out by the wind. Where last year was a hollow there may now be seen the beginnings of a flora, or again the flora of a former year may have been buried out of sight. The dune-complex, then, is not only a maze, but also a restless maze.

It might seem impossible to unravel the tangled threads of the dune-complex; it is, indeed, impossible to write the details of its history. There is, however, a simplicity in the complexity. While little dunes advance in all directions, the complex as a whole advances in the direction of the prevailing wind. While there are troughs at all angles, the main troughs are likewise in the direction of the wind. The complex is like a river with its side currents and eddies at many points, but with the main current in one direction.

It has already been stated that the windward slope of an advancing dune is very gentle, averaging perhaps about 5°. That portion of the windward slope up which the main wind currents pass is also trough-shaped and may be called a wind-sweep. *Fig. 7* shows a small trough-shaped wind-sweep at Beaver island; the direction of advance is from the foreground to the background. In the path of the wind there may be seen dead branches, the remnants of a vegetation that has been swept away. In the background are small dunes which have been formed by sand carried along the trough by the wind. A wind-sweep more characteristic of the dune-complex is shown in *fig. 17*. Here, likewise, the prevailing wind direction is up the gentle slope away from the foreground. At this particular place there is in reality much more of a trough than is shown in the photograph, since there is a conspicuous rise both at the right

and at the left. Just beyond the pines in the background there is a steep pitch downward, the advancing lee slope.

The most remarkable wind-sweep at Dune Park reaches down almost to the water level, appearing like a cañon, by reason of its steep sides from ten to twenty meters in height. This sweep, unlike most of the troughs, is curved so that a wind entering it as a northwest wind becomes a west and finally a southwest wind, and actually contributes to the advance of a dune toward the lake, as will be discussed more fully at another place in connection with *fig. 10*. The concentration of the wind energy which these gorge-like wind-sweeps permit is something remarkable. At no place is the destructive power of the wind upon the vegetation felt more keenly than along the sides of these deeper wind-sweeps. The foreground of *fig. 22* shows the upper part of one of these troughs, and gives a vivid impression of the wind's destructiveness.

The advancing lee slopes, as has been previously mentioned, have a gradient in the neighborhood of 30°. The slope is exactly that at which sand, whose grains have the size and cohesiveness there found, will lie. *Figs. 9, 13, 14,* and *15* give some conception of the striking features presented by a landscape of which an advancing dune forms a part. Nowhere can there be a sharper line in nature, nowhere a more abrupt transition. The height of these slopes above the country on which they are advancing varies from almost nothing up to thirty meters at Dune Park. The Glen Haven dunes are far more imposing, since there is an almost unbroken line of advance for four kilometers, while the average height is from thirty to sixty meters above the territory on which they are encroaching.

The vegetation of the complex proper is exceedingly sparse. In the winter it appears almost a barren waste. The one plant which seems to be at home in all locations, whether wind-sweeps, exposed summits, or protected lees, is the bugseed, *Corispermum hyssopifolium*. This plant is an annual, and has been previously mentioned as a tenant of the beach and the beach dunes. The bugseed is shown in several of the photographs, but best in the

FIG. 8.—Group of cottonwoods (*Populus monilifera*) at an exposed position on the dune complex at Dune Park. Exposure of roots, due to denuding action of the wind. View taken in winter.

left foreground of *fig. 12*. The seeds are winged and readily dispersed by the wind. Furthermore they germinate rapidly during wet spring weather. This power of rapid germination is a necessary condition of success, since the surface layers of sand dry off very quickly after the wet weather has ceased. The plants are obliged not only to germinate rapidly but also to send roots deep enough to reach beyond the surface desiccation. Even this perfectly successful plant species is often absent from large areas on the dune-complex, probably because of the difficulty which the seeds meet in finding lodgment. It is only an exceptional seed which is allowed to remain stranded on the complex, and many of the seeds which succeed in finding lodgment are likely to be buried too far below the surface to permit germination.

Another plant which deserves especial mention is the cottonwood, *Populus monilifera*. The plasticity of this species is remarkable. Normally at home along protected river bottoms, it is yet able to endure almost all of the severe conditions of the dune-complex. Mention has been made of its importance as a dune-former, and *fig. 5* shows a group of cottonwoods on an embryonic dune partially buried by the sand. Photographs might have been secured showing trees, presumably fifteen meters in height, buried up to the topmost branches and yet alive and vigorous. *Fig. 8* (taken in the winter) shows a vigorous clump of trees, high up on the dune-complex, with their roots exposed by reason of the removal of the sand from around them. Much more striking examples than this have been seen of living trees standing high up in the air, and yet with no apparent injury. In one respect the cottonwood is a hardier plant than Corispermum; it is a perennial and hence passes the winter on the dunes. In the summer the winds are much more moderate, and the chances of being covered or uncovered are more remote.

Two grasses are more or less at home at many places on the complex, *Ammophila arundinacea* and *Calamagrostis longifolia*. Of these the latter is the hardiest and most typical of exposed positions, such as shown at the left in *fig. 23*. The tenacity with

which Calamagrostis holds its ground has already been mentioned. On the Glen Haven complex, Ammophila is particularly abundant. In some places it is so thick and green as to look almost like a field of grain from a distance; yet even here, the luxuriant growth is only in the protected places, and none at all is found in the most exposed situations.

The reasons for the scanty plant life on the exposed portions of the dune-complex are not far to seek. First of all it is not due to the scarcity of water in the soil. Even after a long period of drought in summer, the sand is cool and moist at a short distance below the surface. The upper dry layers of sand act as a non-conductor of heat and prevent the evaporation of the water that lies beneath. The height of the underground water level beneath the dunes was not ascertained. Indeed it is not at all necessary to determine where this level actually resides, since there is enough water far above it to support a luxuriant vegetation, if that were the only factor concerned.

In spite of the water supply in the dune sand, the scanty flora of the complex is characterized by the possession of the most pronounced xerophytic adaptations to be found in this latitude. These xerophytic structures will be discussed in the second part of this paper. At this point it is necessary only to state that in the main they are to guard against excessive transpiration, such as is induced by the unusual exposure to wind, heat, and cold. In a certain measure one might attribute these xerophytic adaptations to an insufficient amount of water in the soil, since, were they absent, the soil water would soon be used up. But it is much more important to discriminate, as ecologists are now coming to do, between conditions in the soil and those in the air. A plant may have its roots in the water and yet be exposed to a xerophytic air; in that case the aerial organs will be provided with xerophytic adaptations, as is the bulrush. Schimper, in his recent plant geography, goes still farther and calls some plants hygrophytic at one season and xerophytic at another. Perhaps the ultimate definition of a xerophyte will be a plant that is endeavoring to reduce its transpiration.

Directly or indirectly, the wind is the factor primarily responsible for the scarcity of vegetation on the dune-complex. Incidentally, as has been stated, the wind dries up the soil and increases transpiration. Incidentally, too, the mechanical action of the wind in connection with the sand-blast is destructive to vegetation. The cardinal destructive influence of the wind, however, consists in its power to cover and uncover the dune plants. Two plants have been referred to as peculiarly well adapted to dune life, Corispermum and Populus. The former is a small herb, and unable to endure either covering or uncovering to any great extent. This plant, however, is an annual of short duration and does not exist during the periods of the greatest wind activity.

The cottonwood, which has been shown to be best fitted to withstand the instability of dune conditions, might be expected at first to grow in abundance there. It has almost unlimited powers of endurance in all conditions of exposure; it may be covered to the upper branches, or may have its roots uncovered to a depth of two or three meters, and yet flourish. Its failure to make any considerable headway on the complex is due partly to its relative inability to extend its area by vegetative propagation, partly to its short life cycle, and partly to the impossibility of germination. Thus a group of cottonwoods, which germinated when the conditions were more favorable and have been able to withstand the severe environment of the dune-complex, cannot appreciably extend their area, nor can they live for many years. New trees cannot take their place, because of the inability of the cottonwood seed to germinate on the higher exposed portions of the complex. These seeds sprout much more slowly than those of the bugseed, nor could the young plants withstand the winter conditions on the complex, even should they germinate. Furthermore, the likelihood of any considerable lodgment of cottonwood seed is excluded by their light cottony appendages.

3. *Encroachment on preexisting plant societies.*

Those who are at all familiar with wandering dunes are acquainted with their power to destroy vegetation in the path of their advance. This, indeed, is to many people the most conspicuous feature of a sand dune area, because it often becomes a feature of the greatest economic importance. The effect of an advancing dune upon the preexisting vegetation varies greatly as conditions vary. The most important factors are the rate of advance, the height of the advancing dune above the territory in its path, and the character of the vegetation that is encroached upon.

The rate of advance is, of course, a decidedly variable factor, since all rates, from nothing up to the maximum rate, may be found along nearly all advancing lee slopes. At a given point the rate varies greatly during different seasons. An advancing portion may become checked and a checked portion may advance again, as wind-sweeps are clogged up or opened once more. The multiform changes on the complex; each and all, affect the rate of advance to a remarkable degree. Attempts have been made to measure the maxima of advance at Dune Park, but a sufficient time has not elapsed as yet to allow of any satisfactory conclusions. In November 1897 a stake was driven at the basal edge of a rapidly advancing lee slope. The height of this stake above the ground was a little more than a meter. In May 1898 the stake was nearly covered, and it could not be found at all in July. At this point, therefore, the vertical component of advance amounted to a meter in six months; the horizontal component, of course, was greater still, since the angle of slope was about 30°. The general statement may be made for the Dune Park complex that the maxima of advance are to be measured in decimeters or meters per annum, rather than in centimeters or decameters. No estimates can be given for other localities. In all probability the Glen Haven dunes move more slowly, since the slopes have a much richer vegetation.

The height of an advancing dune above the territory in front

FIG. 9.—General view at Dune Park, showing the encroachment of a dune on pools, swamps, and forests. Dune crest in the left background, oak dunes at the right. Wind ripples in the foreground. View taken in winter.

FIG. 10.—A doomed forest of basswoods, etc., at Dune Park. Dunes encroaching from all sides, but somewhat slowly; dune at right advancing in the direction of the prevailing wind. Thicket of basswood, dogwood, etc., at the left background. Subsequent vegetation in the foreground (grape at right, chokecherry at left).

of it is a very important factor, inasmuch as it often determines the life or death of a flora. At Glen Haven, where the advancing dunes are from thirty to sixty meters high, no preexisting vegetation can survive the burial which awaits it. At Dune Park, where the crest is never as much as thirty meters high, vegetation sometimes survives. This survival is determined chiefly by the nature of the vegetation, and the succeeding paragraphs will have to do with the struggle between dunes and floras at Dune Park.

The advancing dunes at Dune Park encroach now upon a swamp, now upon a forest. *Fig. 9* shows how these forest and swamp conditions alternate. In the right foreground is a pool, surrounded by bulrushes. Toward the center of the photograph there is a ridge tenanted by pines and oaks, then another swamp and another ridge. *Fig. 10* shows a very interesting phenomenon. At the center is a deep trough, surrounded on all sides by advancing dunes. This trough has never been a wind-sweep, but was made by the piling of the sand all about it. The flora in this depression is not a typical sand-dune flora, although surrounded by such on all sides. It is a mesophytic island in a xerophytic sea. The dominant trees in this little group are the basswood, *Tilia Americana*, and the ash, *Fraxinus Americana*. Although the basswood is common on the arrested dunes, this plant society is quite evidently a relict of a larger area developed under more genial conditions. The lake is toward the right, and the dune on that side is advancing with some degree of rapidity. The dune to the left is pushed forward in the main by the action of southerly winds, and moves quite slowly. This dune, however, is at the upper end of the curved wind-sweep previously mentioned, so that northwest winds contribute to its advance. Thus it becomes possible for the same wind to cause the advance of two dunes toward each other and hasten the burial of a flora. The advance of all dunes at this point is relatively slow, as is shown by the comparatively abundant vegetation on the advancing slopes. This vegetation is not a relict of the past. The advancing dunes completely destroy

all of the preexisting vegetation at this point. In a few more years, unless conditions change, there will be nothing left at the surface by which one may interpret the history of this dying plant society.

The encroachment of a dune upon a forest is shown in *figs. 11* and *12*. The forests in this vicinity consist principally of the scrub pine, *Pinus Banksiana*, and the black oak, *Quercus coccinea tinctoria*. Neither of these trees can survive any such degree of burial, as can the cottonwood. The oak, especially, succumbs long before the entire tree is buried; the dead trees along the dune margin in both pictures are oaks. *Fig. 12* shows a pine that is half buried, but apparently as vigorous as ever. The dead trees in *figs. 15* and *16* are mostly scrub pines, and they seem to show no greater adaptation to their new surroundings than do the oaks. There appears to be a wide range of individual adaptation in pine trees, some dying almost as soon as the dune reaches them at all, while others are nearly as resistant as the cottonwood. In both pines and oaks the first obvious sign that the tree is waging a losing struggle is etiolation. The living trees along the margin (as in *figs. 11* and *12*) rarely have a dark green foliage. In most cases the leaves are yellowish green, and in some cases almost white. Nor are the leaves as numerous or large as on healthy trees.

Such tree groups, as are shown in *figs. 9*, *10*, *13*, and *14*, are doomed to an inevitable death. The length of life allotted to them in the future depends almost entirely upon the rate of the dune's advance. There are some evidences in favor of the view that an individual pine tree can endure a deeper covering before death ensues, if the rate of advance is slow. *Fig. 12*, which represents a half buried pine that is still vigorous, was taken at a point where the advance is relatively slow. *Figs. 15* and *16*, on the other hand, where the pines were soon killed, represents one of the most rapidly advancing dunes at Dune Park. Thus the individual adaptation referred to in the preceding paragraph may be in part delusive. Perhaps the trees are able to adapt themselves more fully, and hence undergo a greater degree of

FIG. 11.—Encroachment of a dune on an old and long-established oak dune at Dune Park. Dead oak trees at the margin.

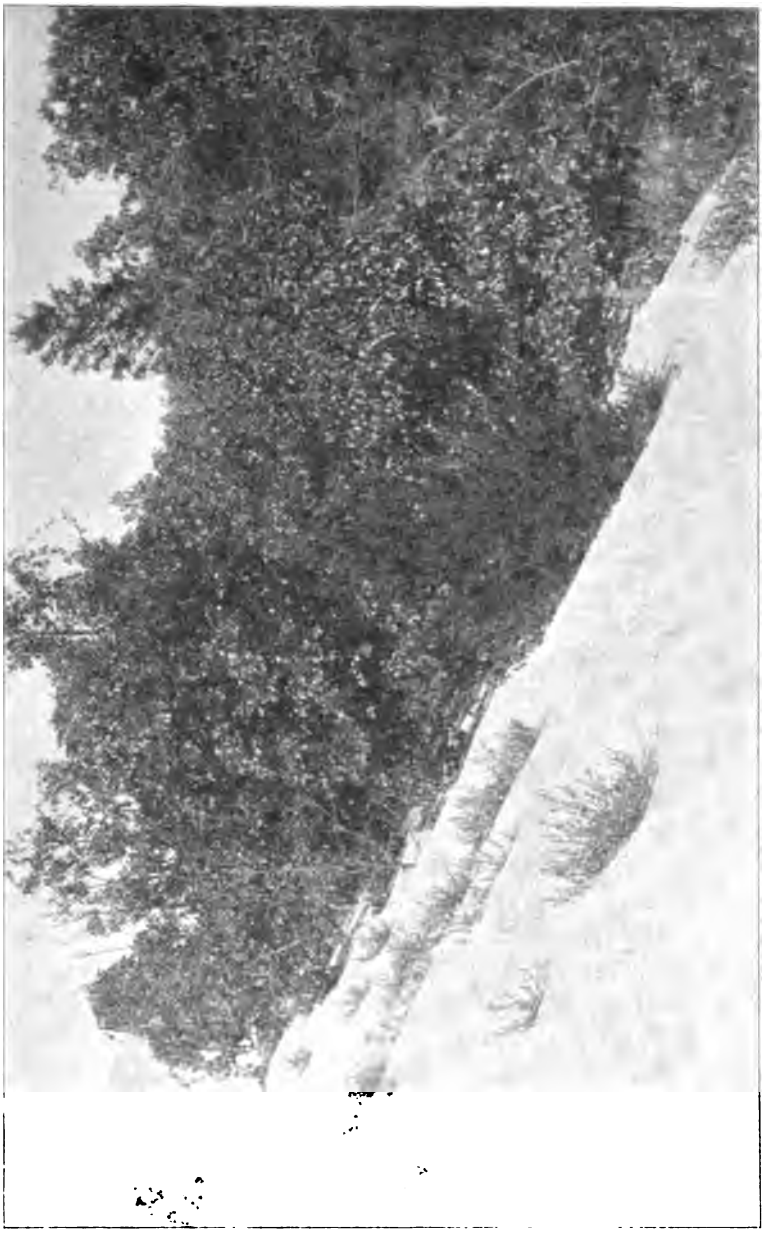

FIG. 12.—Encroachment of a dune upon an oak forest at Dune Park. Bugseed in the left foreground. Half buried but vigorous pine at the center. Dead oak trees at the margin.

covering before they die, where the advance of a dune is comparatively slow. Sometimes (as in *fig. 11*) the territory toward which the dune advances is higher than the dune itself. In such a case the advancing dune is checked. If the entire area in front is higher than the dune, the sand gradually accumulates until the altitude is great enough to permit another advance. When, however, a ridge meets the advancing dune at right angles (as in *fig. 9*), the dune's course is deflected to either side. If the ridge is high enough, some of the trees may be able to escape the fate of their associates. The pines in the background of *fig. 17* probably represent a portion of the flora at the top of one of these ridges.

At Glen Haven, as has been stated, the forest vegetation readily succumbs, because of the great height of the advancing dune. The forests are mainly of two types, the maple or the arbor vitae. The maple forests have a dominance of *Acer saccharinum*, and represent the most common type of mesophytic forest in that part of Michigan. The arbor vitae forests are in reality swamp forests, and the most typical trees present there are *Thuya occidentalis*, *Betula papyrifera*, and *Fraxinus Americana*. The line of dead trees along the margin of the advancing dune (as shown to a slight extent in *figs. 11* and *12*) is particularly striking where there is an encroachment upon a maple forest. Sometimes the hemlock, *Tsuga Canadensis*, grows with the maple and shares its fate. At one point the dune encroaches upon a forest of *Pinus Banksiana*, and the results are precisely as at Dune Park.

Dunes that are encroaching upon forests may be found along the entire coast, though their best development is in association with an extensive dune-complex, as at Dune Park or Glen Haven. The burial of forests was observed at Frankfort, Muskegon, and elsewhere, and is a relatively common phenomenon. In closing up the treatment of the forests, the general statement may be made that an advancing dune destroys the entire forest vegetation. Where this rule meets with any exception, it is an exception that in no real sense invalidates the main proposition.

The encroachment of a dune upon a swamp is of less common occurrence than encroachment upon forests, because forests are so much more common than swamps along the lake shore. The best examples of dunes advancing on swamps were seen at Dune Park, where there are a number of swamps that run more or less parallel with the lake shore. *Fig. 9* gives a good impression of the general appearance of things in the vicinity of Dune Park. In the foreground is a pool and bulrush swamp upon which the dune is encroaching. Beyond the wooded ridge at the center is another swamp of the same type, which is suffering the same fate. In the distance there can be seen the crest of a dune, which is advancing upon a chain of forest-clad hills.

The dune which is shown in the foreground of *fig. 9* encroaches upon a pool in which there is an abundance of aquatic plants, such as *Nymphaea odorata*, *Nuphar advena*, and *Pontederia cordata*. These plants are soon destroyed, of course, but it is surprising how long it is before they die. Leaves of Nymphaea and Nuphar have often been seen raised above the sand, a meter back of the present margin of the pond. These plants must have been partially buried for some weeks, and yet the leaves were scarcely blanched at all. Indeed, an oak tree buried to an equal relative depth would have succumbed entirely. Around the margin of the pool is a luxuriant growth of the bulrush, *Scirpus lacustris*. This plant soon gives up the struggle, etiolation being present when only the basal portion of a stem is buried. The appearance of the bulrush is often striking by reason of the fact that there are etiolated rings alternating with green rings of stem tissue.

Fig. 13 shows the encroachment of a low dune upon a sedge swamp. The beachlike fringe of sand at the base of the dune is peculiar to dunes that encroach on swamps. Considerable sand rolls or is blown beyond the base of the steep slope. Under ordinary conditions this sand is blown away, but as soon as it reaches the wet, swampy ground, it becomes moist, and hence remains for a time as a fringe to the dune. The plants of a sedge swamp are unable to adapt themselves to a dune environ-

FIG. 13.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a sedge swamp and pine bottom. Complete destruction of preexisting vegetation. Beachlike fringe of moist sand at the base of the dune.

FIG. 14.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a swamp and pine bottom. Pocket in the dune with pines. Dogwoods on the slopes. View taken in winter.

ment, and quickly succumb. *Fig. 14* shows a dune advancing on a more mesophytic flora and on a group of pines. The effect here is also destructive, in the main. An interesting pocket in the dune, in which there is a group of pine trees, appears in this figure.

One of the most remarkable phenomena seen in the dune region is shown in *fig. 15*. A dune about twenty-five meters in height is advancing with considerable rapidity upon a bulrush swamp. This swamp is more or less continuously surrounded by a marginal fringe of willows and dogwoods. The bulrushes are quickly destroyed, but the dogwoods and willows have thus far been able to remain not only alive but luxuriant. In order to keep above the sand, these plants are obliged to lengthen their stems far more than is ever the case under normal conditions. Already some of these plants have twice and three times their normal stem height. The buried portions of the stems, particularly of the willows, send out roots almost as soon as they are buried. These plants, therefore, become more and more independent of the deeper soil in which they first grew, thus escaping one of the greatest dangers that was mentioned in connection with many tenants of the embryonic dunes.

Three species have been found that are able to adapt themselves almost immediately to a dune environment, *Salix glaucophylla*, *S. adenophylla*, and *Cornus stolonifera*.[3] The taller shrubs in *fig. 15*, as at the left of the center, are *Salix adenophylla*. The lower shrubs are dogwoods or glaucous willows. *Fig. 16* shows a group of the latter two species growing together. How long these plants will be able to endure is a question that cannot now be answered. The conditions become severer each year, because of the necessity for increased stem elongation, and also because the plants are constantly rising above the protected position in the lee of the dune. At no place is the destructive

[3] Some of the *Cornus stolonifera* may prove to be *C. Baileyi*. These two species certainly intergrade in the dune region. The pubescence character is largely a question of habitat. The best determinative character is the stone, and, judged by this, nearly all specimens examined, whether from the swamps or from the dunes, were *C. stolonifera*. See BOT. GAZ. 15: 38, 86–88. 1890.

action of the wind greater than at the summit of an advancing lee slope.

The encroachment of a dune upon an open swamp or a body of water is seen occasionally along the Michigan shore, as at Grand Haven. In no case, however, were any facts obtained that added anything essential to those given above. In concluding the section on dune encroachment, it may be said that the only conspicuous case of the survival of members of a pre-existing flora is furnished by the swamps. It may at first seem a surprising fact that the plants which are able to adapt themselves to the intensely severe conditions of an advancing dune are hydrophytic willows and dogwoods, rather than mesophytic oaks, basswoods, and maples, or xerophytic pines. Such a view as this comes from a misconception of the change that is needed in the life-habits of the plant. The relation to the soil water is not conspicuously altered, or at least not rapidly altered. It is true that the elongating stem makes it more and more difficult for the plant to draw water from the original root system; but in the case of the willow, at any rate, this is counterbalanced by the development of new roots along the buried stem, which allow the plant to utilize the moisture in the sand. The trees mentioned above are unable to send out such roots, and here, at least, is one possible source of their failure.

There is another line along which the solution of this problem of adaptation may be sought. A number of ecologists in later years have commented on the xerophytic structures of many swamp plants. These structures are not to be found in all swamp plants, but are particularly well-marked in plants of undrained swamps, *e. g.*, peat bogs. Schimper even goes so far as to regard peat bog plants as xerophytes, because the humus acids in the soil make it difficult for plants to obtain the requisite amount of water. Consequently peat bog plants have worked out xerophytic structures to reduce the transpiration. All of the swamps at Dune Park are undrained swamps, and may be called potential peat bogs. The chemical nature of the soil is such that the plants have doubtless adapted themselves to all of the essen-

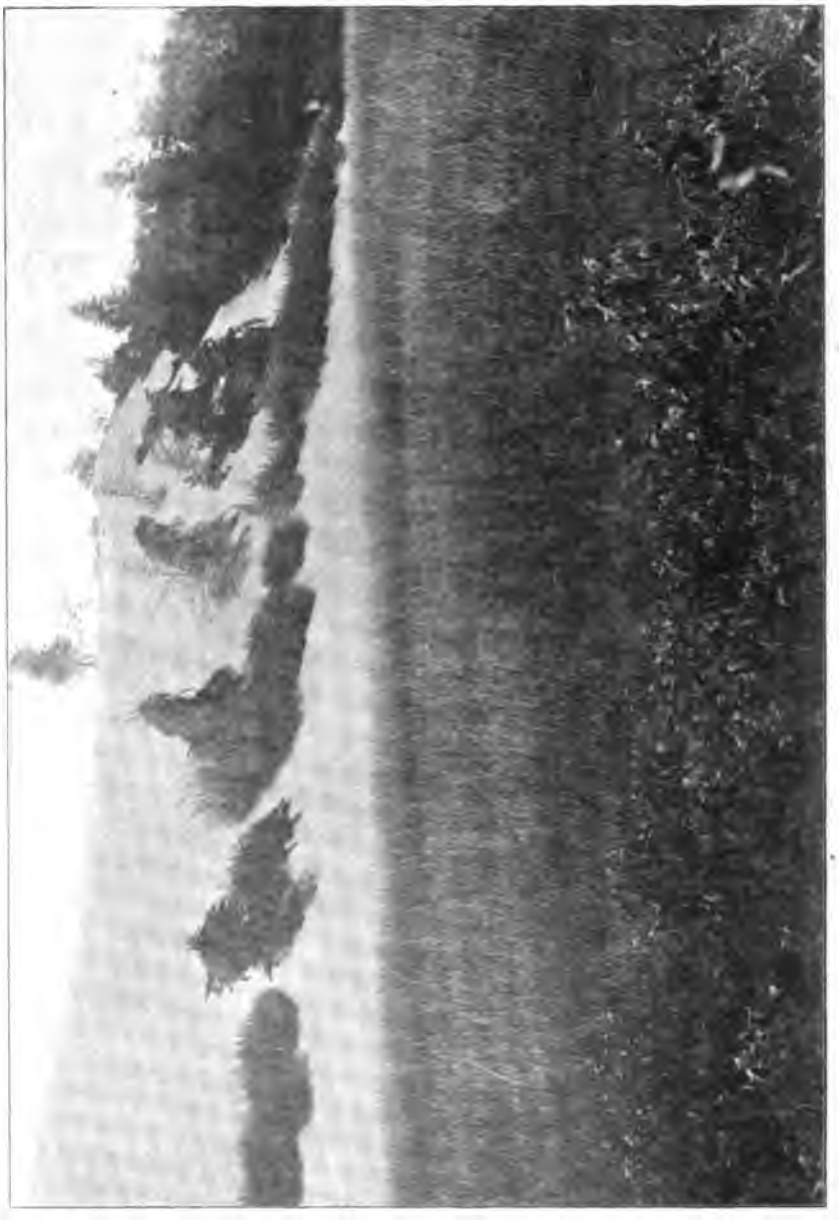

FIG. 15.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a bulrush swamp, which has a marginal row of willows and dogwoods. Death of the herbs and pines, but survival of the shrubs through vertical elongation, enabling them to rise above the sand.

FIG. 16.—Section of the lee slope shown in *fig. 15*. Dogwood and glaucous willows at the center (antecedent). Scattered dead pines. Subsequent vegetation consisting of trailing and climbing grapevines, cedar, and bugseed.

tial conditions of a xerophytic life. The partial burial of these plants by a dune results, as has been seen, in no rapid change of relations with the water in the soil. The aerial organs, however, are exposed to a greater degree of light and heat by reason of their proximity to the sand. Thus the tendency to transpiration is increased, but the plants may be able to keep it within bounds through the xerophytic structures that have already been worked out in a swamp environment. It is likely, too, that these structures become more and more xerophytic as a result of life on and in the dune.

The theories that have been exploited in the preceding paragraph find, at least, a partial confirmation. The leaves of the three successful species have more or less pronounced xerophytic structure. The leaves of the dogwood are quite strongly pubescent. The willows, however, are more decidedly xerophytic. The leaves of *Salix adenophylla* are very hairy, and the cuticle is thick. *Salix glaucophylla* has leaves with a very thick cuticle, and coated on the under surface with a dense layer of bloom. In the dune form of this latter species the leaves are notably thicker and the bloom more dense. It is the author's intention to make a careful comparative study of the anatomical characters of these plants, and make report in the second part of this paper. All three of the species named above have a remarkably wide range of habitat, occurring on embryonic dunes, arrested dunes and heaths, as well as in swamps and on lee slopes. These shrubs may grow at almost any altitude and show a surprising independence of the water level in the soil. There seems to be scarcely any doubt, therefore, but that these species are naturally adapted to a xerophytic life, and that, when the occasion arises, still further xerophytic conditions can be met successfully.

The success of the willows and dogwoods on the dunes may be due, in part, to yet another characteristic. It is well known that swamp plants are provided with extensive adaptations to promote aeration. This need is especially apparent in undrained swamps, where the gases necessary for the underground tissues

and organs have to be almost entirely supplied from above the surface of the soil. It is in these undrained swamps, too, that the accumulation of peat is so rapid. It seems rational, then, to suppose that tenants of undrained swamps, by adapting themselves to prevent suffocation, have also adapted themselves to withstand burial by sand without injury. Just what is the cause of death, when plants are partially buried by the soil, is, so far as the author knows, an unanswered question. A wide field for anatomical study and physiological experiment lies open along this line. In the meantime the notion that plants of undrained swamps are better fitted to suffer partial burial than are other plants may remain as a tentative theory.

In considering the formation of secondary embryonic dunes, mention was made of *Potentilla Anserina*, *Cephalanthus occidentalis*, and *Polygonum Hartwrightii* as dune-formers under certain conditions. Potentilla and Polygonum are extensively creeping herbs, while Cephalanthus is an erect shrub. All three are swamp plants naturally, and yet able, as has been said, to build low dunes of a slow growth. In like manner they sometimes remain living for a time when a wandering dune encroaches upon them. They are especially plastic where the advance of a dune is relatively slow. Among these plants Potentilla seems to be the most adaptable to dune conditions. Another swamp plant that shows a surprising degree of plasticity is *Hypericum Kalmianum*. This shrub is very common in the undrained swamps of the dune region, and very often finds itself in the path of an advancing dune. Hypericum, like Salix, often forms a marginal fringe about a swamp, and miniature lines of this shrub are frequently to be seen toward the base of an encroaching dune, resembling the line of willows and dogwoods shown in *fig. 15*. Of course, Hypericum has nothing like the plasticity and endurance of Salix; nevertheless it may live for many years if the dune advances slowly. Its capacity for vertical elongation is much less than that of Salix or Cornus, so that a rapid advance would soon cover the plants and cause their death. Near the South Chicago beach is a pool with a dense vegetation of

Scirpus pungens about its margin. This plant has served to collect a small amount of sand, and is forming a low secondary dune. Although a large portion of each shoot is covered by the sand, there is as yet no sign of etiolation on the aerial parts of the plant.

Since the highest portion of a wandering dune is close to its advancing front, it is evident that a buried forest will gradually become uncovered, as the dune passes on beyond. No scene in all the dune area is more desolate than such a place. It is a veritable graveyard, where the corpses once buried are exposed again. *Fig. 17* shows a pine graveyard which has had a history like this. In the background are several living pines, presumably members of the same forest with the others. Their position at the summit of a hill permitted them to survive, while those at lower levels were buried by the sand. The uncovered pine trunks are directly in the path of the main wind currents, and hence are subjected to the severest action of the sand-blast. The trunks are carved and battered away until the last remnant of the old vegetation passes away forever.

Graveyards similar to those at Dune Park occur on the extensive dune-complex at Glen Haven. The commonest dead tree there appears to be the arbor vitae, though there are occasional dead trees of birch and ash. In addition to the trunks of trees, there is an abundance of resurrected soil lines at all altitudes on the complex. These black streaks in the sand vary greatly in depth and persistence. Doubtless the organic matter thus exposed is sometimes utilized by the scanty vegetation on the complex, but more commonly it is rapidly scattered by the winds.

4. *Capture of the dune-complex by vegetation.*

The capture of a dune by plants may begin within the dune-complex itself or along its margin. In either case the first appearance of the advancing vegetation is commonly in the lower places toward the water level. The reasons for this fact are obvious. These low places are well protected from the wind;

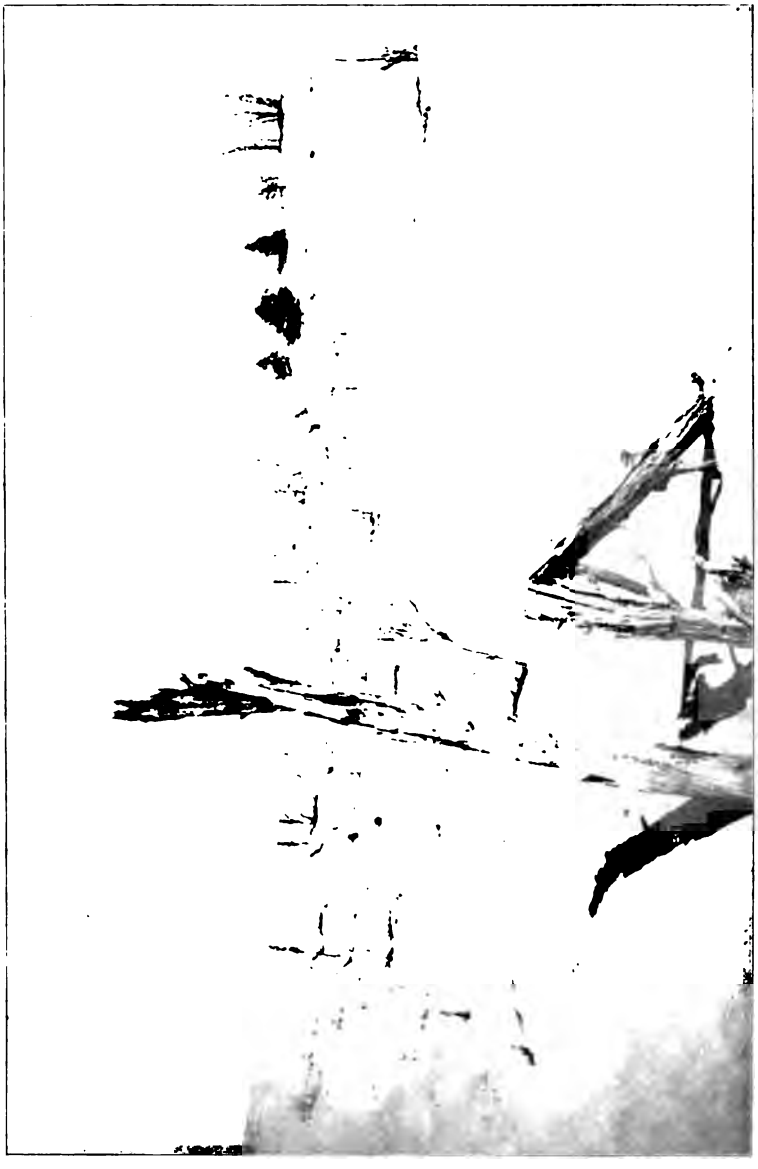

FIG. 17.—Pine graveyard at Dune Park. Forest once buried and destroyed; the dead trees now exposed again. Surviving members of the old pine forest in the background. This area is now a gentle windward slope, and has been converted into a wind-sweep. Carving and battering of the old trunks by sand-blast.

there is no danger, therefore, of any sand-blast action on the plant organs nor any removal of soil from around the roots. When the growth begins at the foot of an advancing lee slope, there is, however, considerable likelihood that the plants will be covered by the sand. It is this fact which prevents the capture of a rapidly advancing dune; the vertical growth of the plant must be greater than the vertical component of the dune's advance.

The most important reason for the first appearance of plants at lower levels is the soil moisture. It is the moisture at the surface of the soil which causes to a large degree the lodgment of seeds, and especially light cottony seeds like those of the cottonwood and willow. At the base of the dune shown in *fig. 9*, where it is encroaching on a swamp pool, there is a line of young cottonwoods and willows several inches above the level of the pool. The seeds were blown across the complex by the wind; when they reached the crest of the advancing lee slope, they rolled down to the base together with the sand. The base of the dune is always moist several inches above the surface of the water because of capillarity. As soon as the sand and seeds reached the moist soil near the base, the movement was checked and both found lodgment.

The moisture necessary for the germination of the cottonwood and willow seeds is also furnished at these low places near the water level. The danger of being covered by the drifting sand is much less at this place because moist sand is more compact than dry sand, and because moist sand does not collect about the growing plants. The dune shown in the foreground of *fig. 9*, however, is advancing very rapidly, and it is not likely that the growth of the young plants will be rapid enough to prevent their being covered. In the moist sand at the base of the dune shown in *fig. 9* patches of algæ have been seen, presumably Chlamydomonas, such as have been described in connection with the lower beach. It is doubtful if these algæ are of any significance in the capture of dunes.

If the vegetation gets a foothold at the base of an advancing

slope, it tends to creep up the slope by means of vegetative propagation. At the base of the cottonwood dune shown in *fig. 5*, there may be seen grasses which appear to be creeping up the slope in this manner. It should be borne in mind that such appearances are often deceptive. In this particular instance the appearance would be the same if the dune were advancing and the grasses rising to keep above the sand. In like manner there is doubt with regard to *fig. 16*, as to which vegetation antedates the dune and which is subsequent. As has been already stated, the clump of dogwoods and willows at the center beyond all question antedates the dune; so too, the dead half-buried pines. The annual bugseeds toward the base, of course, are subsequent.

The greatest doubt is as to the frost grape, *Vitis cordifolia*[4]. At the upper right hand there is a luxuriant grapevine climbing over a dead pine. The clumps back of the willows and the trailing vines in front of them are also Vitis. *Fig. 15* shows several large grapevines back of the row of willows. The coarse-leaved vines at the lower right hand of *fig. 10* are also Vitis. It seems incredible that the vines in this last picture should be anything else than subsequent, since the height of the sand above the wooded hollow is more than twenty meters. Then too the Vitis vines are very abundant all along the coast on the naked dunes, but are rarely found elsewhere. On the dune shown in *fig. 15*, for instance, there are two willows, a dogwood, and the grape growing together. The dogwood and one of the willows are very common in the adjoining swamp, while the grape was not found there at all. On the other hand, no grape seedlings have as yet been found in any such location. While much further study is needed in this connection, it seems likely that Vitis is subsequent to the dune.

A little above the center to the left in *fig. 16* is a young cedar, *Juniperus Virginiana*. This little plant is several meters up the slope and is unquestionably subsequent. In the left foreground of *fig. 10* is a shrub of the chokecherry, *Prunus Virginiana*, which

[4] The identification here may be questioned; fruiting specimens are rather rare, but prove to be this species so far as examined.

is certainly subsequent to the dune. In fact this shrub is rather frequent in such locations. The author does not feel clear as to the conditions which permit the germination and development of these plants in such unstable situations, for it must be remembered that the advance is rather rapid in all cases. No seedlings of the cherry, grape, or cedar have been seen in any such location. It may be that the germination and early growth took place when there was a temporary lull in the advance or during extremely moist seasons. The question cannot be fully solved without a careful study of marked plants for several seasons.

So far as the capture of the dune is concerned, it is a matter of no moment whether the vegetation is antecedent or subsequent. All contribute together to the common end. Of the plants mentioned thus far, Corispermum (shown in the left foreground of *fig. 12*) is of no value in dune capture, because of its annual habit. *Prunus Virginiana* and *Populus monilifera* are rarely abundant enough on lee slopes to be of much value, especially because they have little or no vegetative propagation. The only plants which seem to thrive and increase their area of control on rapidly advancing lee slopes are *Salix adenophylla* and *glaucophylla*, *Cornus stolonifera*, and *Vitis cordifolia*. None of these, however, flourish except on the protected slopes. They are unable to grow along the crest, and hence unable to check the constant advance of the sand.

Vegetation seems to be unable, then, to capture a rapidly moving dune. No such dune has been seen where the vegetation has secured a greater foothold than is represented in *figs. 15* and *16*. This dune is in no sense captured; indeed, its progress is scarcely checked. The more vigorous plants may retain an uncertain foothold for a long time, and again they may not. So long as the crest is unoccupied by plants, the advance will continue almost without hindrance. The life conditions at the crest are so much more severe than on the slope that vegetation is almost certain to be excluded until the advance is checked by physical agencies. For the capture of a rapidly moving dune, a plant species should have the power of rapid germination pos-

sessed by the bugseed, the power of vegetative propagation possessed by the willows, the capacity for growth in height possessed by the cottonwood, or even more than that. The growth of the young plant during the first season should be greater than any of the above, so as to more than counterbalance the vertical component of advance during the period of rest. The life cycle should be of very great length. The plant should be able to endure all extremes of heat, cold, and drought, and all degrees of covering by the sand. No plant species in the Lake Michigan region begins to meet all of these requirements, and, as a consequence, the dunes would advance indefinitely so far as vegetation is concerned.

Various physical conditions tend to check the progress of many dunes. As a dune advances farther and farther from the lake, the effective power of the wind which moves it becomes reduced. The energy is largely spent before the crest of the advancing dune is reached, because of inequalities in its path. The wind commonly builds up other dunes between the lake and the main crest; these dunes serve as barriers, and of course check the advance. Occasionally there are hills in front of the advancing dunes; these check the advance temporarily, at least. The primary cause for a permanent decrease or cessation of movement is the decrease or entire loss of available wind energy. Many wandering dunes never advance rapidly at any period of their life-history. This is because their movement is in some other direction than that of the prevailing wind, or because the full force of the prevailing wind is not directed toward their advance, because of physical reasons. Dunes of this slowly moving type are much more common than the other, and may be seen at almost any point along the entire southern and eastern shore.

Whatever the cause, a slowly advancing lee slope is soon captured by vegetation. The process begins just as described above. Vegetation gets a foothold at the base and creeps up the slope. Antecedent plants, like dogwoods and willows, increase their area by vegetative propagation. Annuals, biennials, and even the hardier perennials germinate and successfully develop at all

points. There are many plant species whose power of vertical growth is greater than the vertical component of a slow dune's advance. This latter condition is always the chief test which determines the vegetation of a lee slope. As the advance becomes slower, more and more plant species are able to get and retain a foothold on the dune.

The capture of lee slopes by vegetation was well seen in all its stages at Glen Haven and Grand Haven. At first the vegetation may be dominantly antecedent, as in the case at Dune Park. More commonly, however, the vegetation is chiefly subsequent from the start, chiefly because the area that is encroached upon contains no plants that are fitted for a dune life. Where there is no antecedent vegetation, the first plant to get a foothold is commonly *Ammophila arundinacea*. Plants that follow in quick succession are *Asclepias Cornuti*, *Equisetum hyemale*, *Calamagrostis longifolia*. Some dunes are almost completely covered with a dense growth of Ammophila. All of these plants are perennial herbs and all but Calamagrostis have very extensive vegetative propagation, so that the capture of a slowly moving dune is a relatively quick process. With these plants there may grow annuals and biennials, but they are of little or no value in dune capture. The commonest of these is *Corispermum hyssopifolium*.

Before many years have passed shrubs and small trees find an entrance and gradually drive out the herbaceous vegetation described in the preceding paragraph. These herbs are all fitted to grow in the most exposed situations, but are not adapted to shade. The shrub vegetation of arrested lee slopes may be partly antecedent, but not largely so. The most common species of shrubs on recently captured slopes are *Cornus stolonifera* (or *C. Baileyi*), *Salix adenophylla* and *glaucophylla*, *Vitis cordifolia*, and *Prunus Virginiana*. With these shrubs young trees of *Tilia Americana* are common. A lee slope thicket of Cornus, Tilia, and others of the above plant species is shown at the upper left hand of *fig. 10*.

All of the species named above occur on arrested lee slopes along the entire coast. The species which are peculiarly char-

acteristic of such habitats are Cornus, Prunus, Equisetum, and Asclepias. These four species are found in other associations, but reach a decided climax here. Ammophila, Calamagrostis, Corispermum, Salix (both species), Vitis, and Tilia are almost as common, but have a much wider habitat range. Ammophila, Calamagrostis, and Corispermum are also found in nearly all plant societies thus far discussed, but they disappear entirely as soon as the vegetation becomes dense. The willows are common in many places on the beach and complex, but they too are ruled out as soon as a real forest vegetation gets a start. Vitis grows also on rapidly moving lee slopes, and remains after the forest has begun. Tilia more than all others looks to the future; as will soon be shown, it is the dominant tree of the first forests that grow on the old lee slopes. With the entrance of the basswood, the true dune conditions and the true dune plants are obliged to pass away.

There are other interesting plants that get an occasional foothold on the arrested lee slopes. At several such places at Glen Haven *Betula papyrifera* was seen. Near Chicago this tree does not grow on the dunes at all, although common along the margins of sloughs. It appears to become more xerophytic northward. Exactly the same is true of *Thuya occidentalis*. Possibly the climatic conditions northward are such as to permit plants that grow normally in protected situations to grow where the exposure is much greater. On an arrested dune at Glen Haven where shrubs for some reason are infrequent, *Solidago humilis Gillmani*, *Aster laevis*, and *Achillea Millefolium* grow abundantly with the herbs previously mentioned.

Before tracing the further growth of vegetation on lee slopes, something may be said of the origin and development of vegetation within the dune-complex. Of course all antecedent vegetation has been long ago destroyed. The capture of the dune must, therefore, be effected entirely by means of plants which germinate and develop on the complex itself. Speaking broadly, the complex is almost entirely composed of windward and leeward slopes. Since the windward slopes are low, it follows

that they cover a much larger area than do the other. Perhaps nine tenths of an ordinary dune-complex is directly exposed to the prevailing wind. The capture of any portion of the windward slope is unlikely, because of the combination of exposure and instability of soil. In the summer a somewhat extensive vegetation may develop, made up largely of annuals and biennials. The most abundant of these plants is *Corispermum hyssopifolium*. Other species are *Artemisia Canadensis* (or *A. caudata*), *Cakile Americana*, *Euphorbia polygonifolia*, *Cnicus Pitcheri*. These plants are commonly more abundant in the deeper wind-sweeps than elsewhere, probably because the sand is moister and more stable in the sweeps than at other places. *Fig.* 7 shows a very characteristic wind-sweep with its vegetation composed of the bugseed and other short-lived plants.

Although the summer winds are much less severe than those of winter, the effects on the vegetation of the wind-sweeps are often conspicuous. Artemisia and Corispermum plants frequently have the sand blown away from their roots and they are thus obliged to lean over on the sand. The stems become much twisted and the whole plant is shorter and more compact than when developed in more protected habitats. Occasional perennials that may germinate in such places rarely live over the winter. The vegetation develops anew each year and no steps toward capture are taken. The conditions on the lee slopes of the complex are much like those on the main advancing slopes. Of course all of the vegetation is subsequent. The conditions are, perhaps, more severe because more uncertain. Large slopes covered with Ammophila are common on the Glen Haven complex. Permanent capture may sometimes result on such slopes, but it is much rarer than at the slowly advancing edges of the complex.

The most important development of vegetation on the complex is in the "blowouts," or hollows produced by the wind. These depressions sometimes reach down almost to the water level and may be as much as thirty meters below the general level of the complex about them. In these depressions the sand

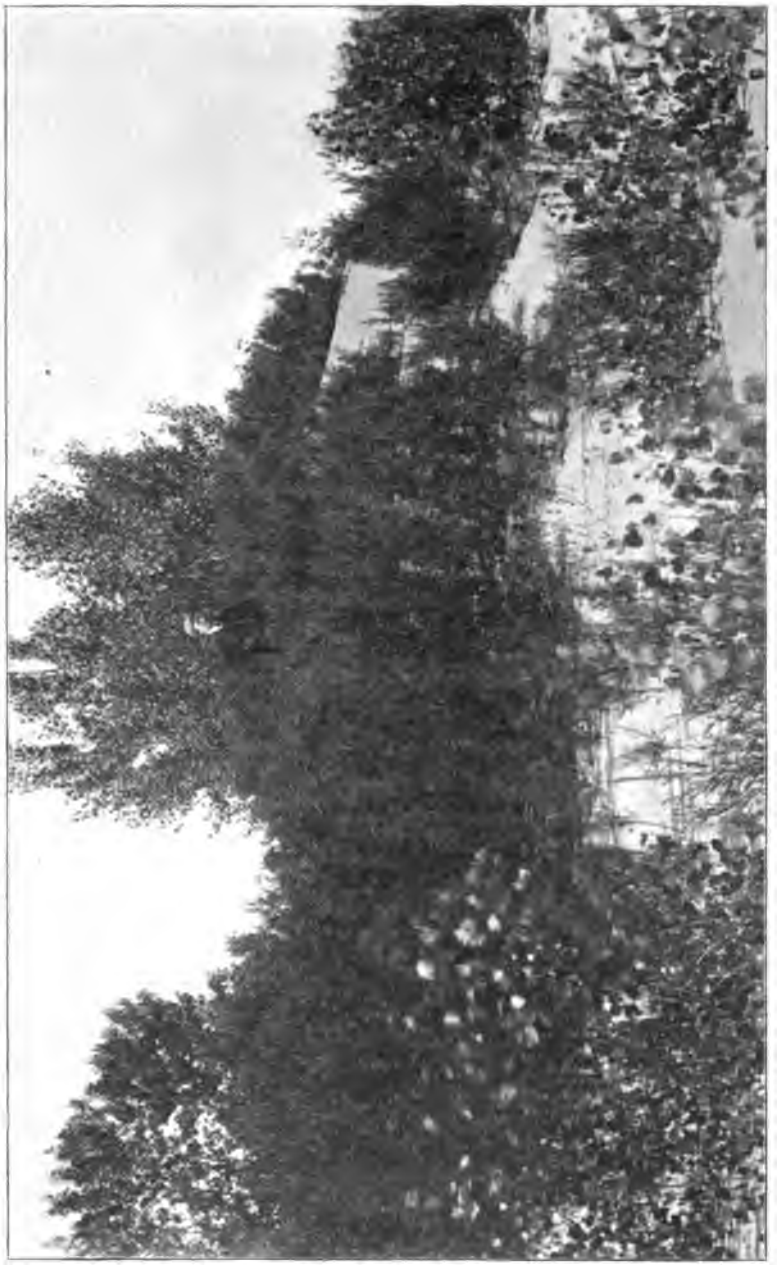

FIG. 18.—Lee slope on the dune-complex at Dune Park, captured by the long-leaved willow, *Salix longifolia*, and the cottonwood (broad-leaved forms). Dense clumps of the willow due to vegetative propagation.

is moist and protected from the severest action of the wind, so that seeds find ready lodgment and a favorable opportunity for germination and growth. The commonest plants observed are the annuals and biennials mentioned just above, and the following perennials: *Populus monilifera*, *Salix longifolia*, *adenophylla*, and *glaucophylla*, *Juncus Balticus littoralis*. Seedlings of the cottonwood and the three willows appear by the thousand, and a large number survive the rigors of the winter. This is the one dune habitat where Juncus and *Salix longifolia* are at all abundant. These two species are marvelously well adapted to inaugurate dune capture. Both of these plants have very extensive powers of vegetative propagation. Rootstocks of this last-named willow often trail along in the sand for ten, twenty, or thirty meters. Thus the plants extend their area up the slopes of the depression on all sides by means of this vegetative increase. *Fig. 18* shows a lee slope on the complex, which has been almost entirely captured in this way. The dense clump of narrow-leaved shrubs at the center is *Salix longifolia*, probably all coming from one or two plants that have spread vegetatively. The broad-leaved shrubs and trees are *Populus monilifera*.

D. THE ESTABLISHED DUNES.

1. *The basswood-maple series.*

It was shown in another place how the steep lee slopes of the slowly advancing dune-complex are first captured by social perennial herbs like Ammophila and Asclepias. Then shrubs like Cornus, Salix, and Prunus grow up and gradually drive out the herbs which grew there first, because they are ill-adapted to the shade. With these shrubs there often develop many young trees of the basswood, *Tilia Americana*. As these trees grow rapidly, it is not long before the thicket becomes a little forest, in which the dominant tree is the basswood. The basswood dune, more than any other type of established dune, is *sui generis*. It is to be found along the entire coast between Dune Park and Glen Haven.

The conditions that determine the development of the wonderfully characteristic flora are very obscure. The basswood dunes are always very steep and relatively near the lake. Unlike all other established dunes there is no approach to a vegetation carpet; the sandy soil is loose and bare and evidently more or less shifting. The movement of the sand is due directly to gravity and only indirectly to the wind. The only obvious condition which favors the rich development of plants is the almost complete protection from the wind.

The trees of the basswood dunes grow as thickly together as trees ever grow, and much more thickly than in any other dune forests. Everywhere the basswood is the dominant tree; no other tree begins to approach it in importance, although *Populus monilifera* is often common. At the south end of the lake *Sassafras officinale* grows with the basswood in abundance. Trees that occur occasionally along the coast in this association are *Quercus coccinea tinctoria*, *Fraxinus Americana*, *Juglans cinerea*, *Ulmus fulva*, *Ostrya Virginica*, *Acer saccharinum*, *Betula papyrifera*, *Abies balsamea*, *Pinus Strobus*, *Tsuga Canadensis*, *Thuya occidentalis*.

One of the remarkable features of the basswood dunes is the luxuriant development of lianas. Scarcely anywhere away from the river bottom forests is there such a development of climbers in this region. *Celastrus scandens*, *Vitis cordifolia*, and *Rhus Toxicodendron* occur almost everywhere. *Ampelopsis quinquefolia* and *Smilax hispida* are not infrequent. The great liana development may be correlated, perhaps, with the dense growth of trees.

Shrubs are abundant about the margins of the miniature forests and in the more open places. Often these may be regarded as relicts of a former exclusive shrub vegetation. *Prunus Virginiana* and *Cornus stolonifera* are the most common tall shrubs, *Rosa Engelmanni* the most common low shrub. At the south end of the lake *Hamamelis Virginiana*, *Ptelea trifoliata*, *Rhus Canadensis*, and *Celtis occidentalis pumila* are common and very characteristic. The only herb that can be regarded as characteristic of this association is *Smilacina stellata*. *Elymus Canadensis* occurs in the open places. Many other herbs are occasionally present,

but there is no necessity for mentioning them. The slopes of the crateriform depression in *fig. 22* have most of the typical plants of a basswood dune. The bare trees are chiefly basswoods, the others pines.

By all odds the most remarkable feature of the flora on the basswood dunes is its decided mesophytic flavor. The majority of the above-named species are usually pronounced mesophytes. Indeed, along the wooded bottoms of the Desplaines river far from dunes and dune influences, the following of the above plants may be found growing together: Tilia, Fraxinus, *Ulmus fulva*, Populus, Celastrus, Vitis, *Rhus Toxicodendron*, Ampelopsis, Smilax, Prunus, Cornus, Hamamelis, Ptelea, and Celtis. Thus half of the entire number recorded above are found in a single river bottom forest. Of the fifteen most characteristic plants of the basswood dunes at the south end of the lake, eleven are found along the Desplaines bottoms; two of the remaining four, Sassafras and Smilacina, are common as mesophytes. Only two of the fifteen, *Rhus Canadensis*, and Rosa, are commonly xerophytic.

Apparently the life conditions on the basswood dunes are anything but similar to those of the river bottoms. The former appear to be xerophytic, the latter mesophytic and inclining to hydrophytic. The soil of the dunes is sand with scarcely any humus at all, and the slight water content is made less by the steepness of the slope. In the river bottom there is a deep alluvial soil rich with humus and with an abundance of water. Nor is the river bottom flora on the dunes the vanguard or the relict of a river bottom flora. At the south end of the lake, at least, the basswood dunes and river bottoms are separated from each other by many kilometers. The likeness of the floras suggests a likeness of conditions in the two apparently very dissimilar habitats. What this likeness is, if it exists at all, cannot easily be seen.

It is this river bottom flora on the dunes that furnishes the best examples of anatomical variation due to habitat conditions. Most remarkable gross variations are found in the leaves of nearly all

FIG. 19.—Summit of a coniferous dune at Dune Park. The trees are white pines. The shrubs in front of them are junipers; those at the left, cedars. The grass in the foreground is Andropogon.

the species. Celtis, a tall tree on the bottoms, is a thorny shrub on the dunes. The tissues, also, are highly modified so as to meet the requirements of the dune conditions. These great variations, not alone in a single species, but in a plant society transported, as it were, from the river bottoms to the dunes, will supply a large part of the material for the second or anatomical portion of this paper. It is also the author's intention to experiment with the river bottom and dune forms of the various species, and endeavor to determine whether or not these changes can take place within a single plant generation.

The development of an undergrowth of shrubs and herbs on the steep basswood dunes tends more and more to stop the sifting of the sand between the plants. The partial decay of the leaves which fall year after year gradually produces a humus. The conditions approach more and more those of the typical mesophytic forest, even though xerophytic dune societies may surround on every side. The growth of the humus permits the development of a low vegetation, consisting of lichens, mosses and forest herbs. The vegetation, shade, and humus conserve the water and cause a mesophytic soil in spite of the slope and sand. Seedlings of other trees, yet more indicative of the shady mesophytic forests than the basswood, make their appearance. The most prominent of these is the sugar maple, *Acer saccharinum*. Scarcely less important are the beech, *Fagus ferruginea*, and the hemlock, *Tsuga Canadensis*. These trees produce the densest shade and cause the extermination of the basswood and its associates. Each vegetation from the original Ammophila to the maple forest, therefore, gives a denser shade than the one preceding.

Accompanying the above-named trees are such typical mesophytic forest herbs as *Hepatica triloba*, *Trillium grandiflorum*, *Epiphegus Virginiana*, and *Arisaema triphyllum*. That the conditions not only in the soil but even in the air are less xerophytic than when the basswood was the dominant tree is shown by the great luxuriance of the vegetation. The trees are just as large as in inland forests and the xerophytic structures that were

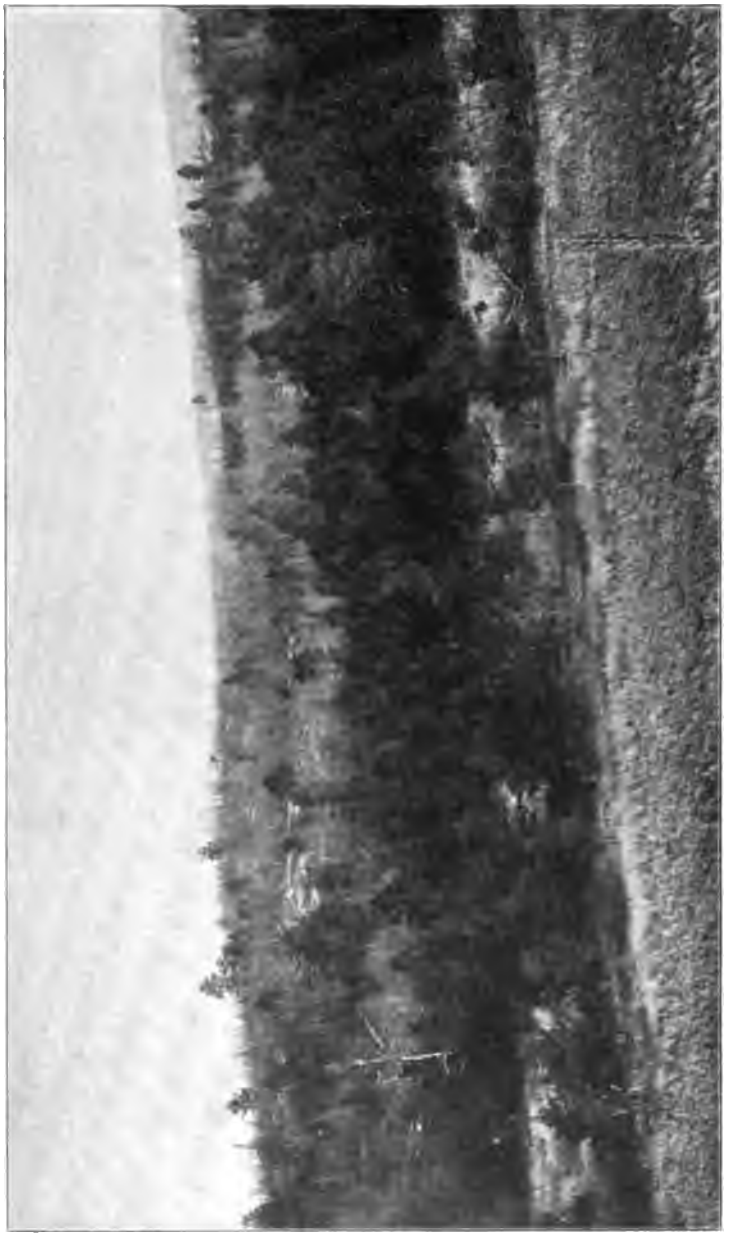

FIG. 20.—North slope of an oak dune at Dune Park, taken in winter, showing scattered pines among the oaks, and an abundance of pines at the lower levels.

present in the basswoods and their associates are quite absent in the maples, beeches, and hemlocks. The air seems to be almost as mesophytic as in the inland forests. The maple and beech forests are not frequent on old dunes at the south end of the lake, but, for that matter, they are not so well-developed anywhere in this region as they are in Michigan. Mesophytic forests on old dunes were seen at Saugatuck, Grand Haven, Frankfort, and Charlevoix. At Frankfort there is a maple forest on the steep slope of an old dune which is as luxuriantly developed as in an inland location. At Charlevoix a hemlock was seen which had over 200 rings, showing the minimum length of time that the mesophytic flora could have existed on the dune. The mesophytic forest is the most permanent of plant societies in the lake region. It may be regarded as the culmination of the series which began with the lower beach.

2. *The evergreen series.*

a. The heath. — The life-history of a windward slope is vastly different from that which has just been described. If one views a region of established dunes from the lake side, he sees a landscape in which evergreens predominate, whereas a view from the land side often shows a decided dominance of deciduous trees. Not only the windward slopes but the summits have an evergreen flora. The key to these facts is exposure to desiccating factors, especially heat, cold, and winds. So far as the soil is concerned, there is but little difference between the conditions on the windward and leeward slopes. In both cases there is a vegetation carpet and a covering of humus. The more gentle slope favors the retention of moisture, though this factor is counterbalanced by the desiccating influence of the wind on the soil. At the south end of the lake the soil of the leeward slopes is drier than that of the windward slopes, because of the southern exposure and consequent drying influences of the sun. Even in this latter instance, the contrast between the floras of the two slopes is tremendous. It is the condition in the air, not the condition in the soil, which determines the difference

here found. Both slopes have a mesophytic soil; the leeward slope also has a mesophytic air, but the windward slope has a xerophytic air.

The heath has several origins but one destiny. It may arise on the slow-growing embryonic dunes, in depressions on the upper beach, on the fossil beach, on gravel terraces, or in

FIG. 21.—Rejuvenated dune on Beaver island. Wind-sweep at the center. Coniferous forests on each side that are not yet destroyed.

pastures. In all cases the dominant plant species come to be one or more of the following: *Arctostaphylos Uva-ursi*, *Juniperus communis*, *Juniperus Sabina procumbens*. The first two are common along the entire coast, the latter only northward. The term heath has been but little used in America, perhaps because we do not have the peculiar Calluna heaths of Europe. The term heath, as here used, may be defined as a xerophytic flora in which there is a dominance of low evergreen shrubs. Warming and Graebner use the term heath much more comprehensively, speaking of moss and lichen heaths and coniferous heaths.

Along Lake Michigan the heath formation becomes more and more prominent northward. A well-marked juniper or bearberry heath is rare at the south end of the lake, while extensive areas are covered by the heath on Beaver and North Manitou islands and on the neighboring mainland.

During the development of a heath, the vegetation partakes of the nature of the formation which preceded it, whether dune or beach or terrace. Before the true heath plants cover the soil, the open places are inhabited more or less abundantly by such plants as *Prunus pumila*, *Salix glaucophylla* and *adenophylla*, *Solidago humilis Gillmani* and *nemoralis*, *Aster laevis*, *Calamagrostis longifolia*, *Smilacina stellata*, *Lithospermum hirtum*, *Artemisia Canadensis*, *Rhus Toxicodendron*, *Rosa Engelmanni*. On fossil beaches and terraces, embryonic heaths often have *Hudsonia tomentosa*, *Andropogon scoparius*, and *Campanula rotundifolia arctica* in addition to the above.

At the center of *fig. 6* there is shown a heath developing on a substratum of embryonic dunes; the bearberry has already covered a large portion of this area with a low heath carpet. *Fig. 24* shows the development of a heath on a fossil beach. In the foreground is a typical fossil beach flora, consisting of scattered grasses, sand cherries, etc. The small scattered tufts are Hudsonia. At the center is a low Ammophila dune, while back of this are patches of embryonic heath, composed of the bearberry and the procumbent juniper. Along the edge of the forest the heath forms a continuous carpet. *Fig. 25* shows a typical juniper heath when fully developed. At the left background the heath is younger and still made up of disconnected patches. *Fig. 26* shows the formation of a *Juniperus communis* heath in a pasture. Since this latter species is more or less erect, while the bearberry and procumbent juniper are creepers, the aspect of the heath shown in *fig. 26* is very different from those shown in *figs. 6* and *24*.

b. The coniferous forests.—Whatever the origin of the heath, it is rarely a climax type along the Lake Michigan shore. It almost uniformly develops into a coniferous forest sooner or

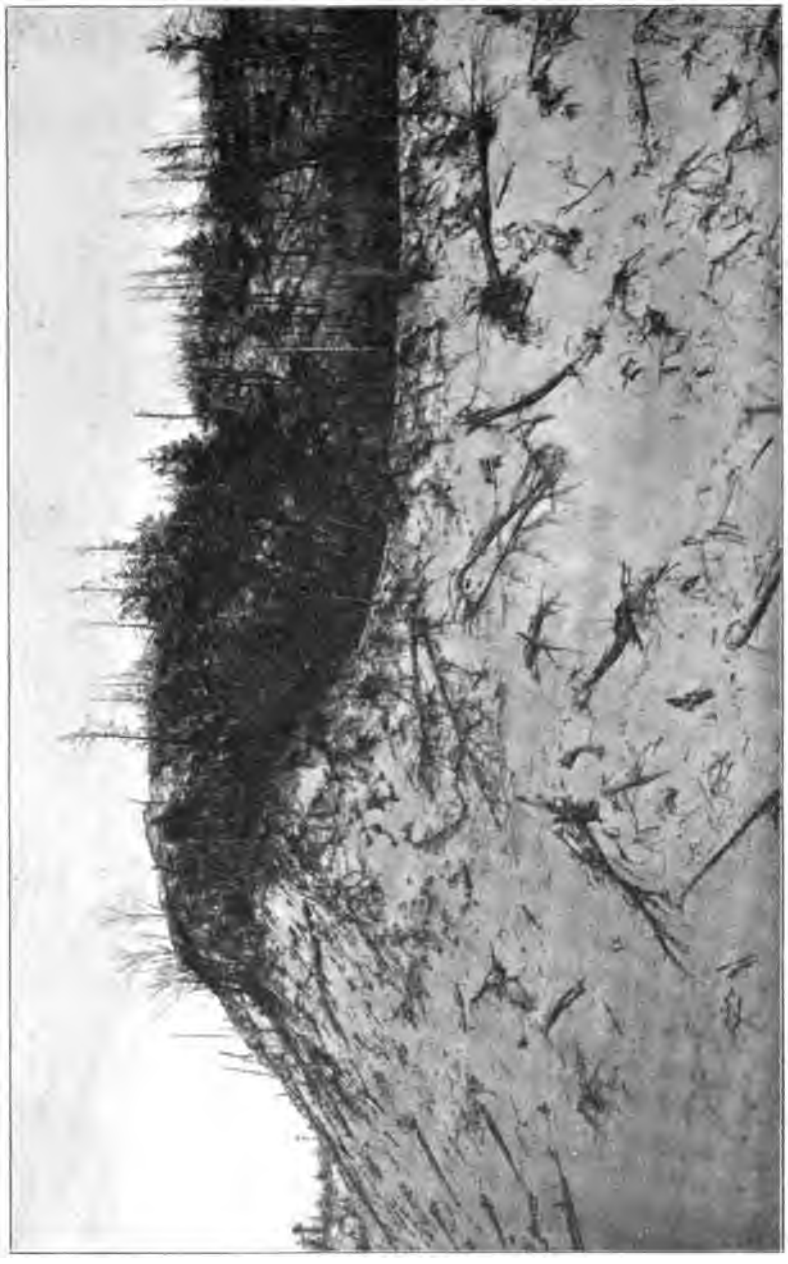

FIG. 22.—Crateriform depression at Dune Park, within which are basswoods and pines in a state of considerable luxuriance. The slope in the foreground is the side of a deep wind-sweep; the development of this wind-sweep brings about the destruction of the flora through the action of gravity.

later. The most conspicuous and extensive forests of this type are on the lakeward slopes, at the summit of these slopes, or at the summit of the taller inland dunes. These forests, like the heath, become more abundant and the growth more luxuriant as one passes northward along the lake shore.

The development of a forest from a heath is easy to understand and can be observed at almost all points. The heath vegetation is dense enough to prevent the tearing up of the soil by the wind, but not too dense for seedlings of various trees to get a start. The dense tangle of junipers and bearberries close to the soil is peculiarly well fitted to protect the trees while small and tender. In a very short time small and scattered trees become conspicuous on the heath. The transformation of a heath into a forest is illustrated by *figs. 24* and *25*. In each case the heath is encroaching on a beach and is being followed up *pari passu* by the forest. The advance of the heath is secured mainly by vegetative propagation, that of the forest by germination of seeds. This fact, together with the need for protection to the seedlings, prevents the forest from overtaking the heath in the struggle for more territory. So far as observed, the heath always precedes the forest, when the latter is developed in an exposed situation.

In the region as a whole, the pines are by all odds the character trees of the coniferous forests, and especially the white pine, *Pinus Strobus*. This tree is found at all places along the coast. At the south end of the lake the scrub pine, *Pinus Banksiana*, is more abundant than the white pine, while at the north end the red pine, *Pinus resinosa*, is often as frequent as the white pine. The distribution of the pines is very surprising. The scrub pine is the most northern of the three pines mentioned, and its farthest known southern limit is about the south end of Lake Michigan. Peculiarly enough, it is far more abundant than all other conifers put together at the south end of the lake, while it is much less abundant to the north along the lake shore. It was not seen at all north of Glen Haven, though it is reported as common inland. The red and white pines have in general a

FIG. 23.—Rejuvenated dune at Dune Park. The basswood is the last remnant of a former forest. Clump of Calamagrostis at the left, showing the tenacity with which its roots hold the sand.

more southern range than the scrub pine, and yet they are more abundant northward along the lake than is the latter. Furthermore, these pines become more abundant absolutely as one goes northward. The red pine was not seen south of Pentwater.

North of Grand Haven *Thuya occidentalis* becomes a frequent member of the coniferous forests; sometimes it becomes as dominant as the pines. The same may be said of *Abies balsamea*, though it was not seen south of Frankfort. *Juniperus Virginiana* is frequent, especially southward. With the evergreens are occasional deciduous trees, especially at protected forest margins; among these are *Betula papyrifera*, *Tilia Americana*, *Populus monilifera*, and *Ostrya Virginica*.

So long as the coniferous forests remain more or less open, the three dominant heath plants, *Arctostaphylos Uva-ursi*, *Juniperus communis*, and *J. Sabina procumbens*, retain their prominence. Of these Arctostaphylos is the most persistent, and may be regarded as the most characteristic plant of the forest undergrowth. There are occasional shrubs in the open places, such as *Shepherdia Canadensis*, *Diervilla trifida*, *Rosa Engelmanni*, *Prunus pumila*. Among the herbs in open places are *Calamagrostis longifolia*, *Aster laevis*, *Smilacina stellata*, *Arabis lyrata*, *Lithospermum hirtum*. Many mosses occur more or less shaded by the evergreens, especially Thuidium and other trailing varieties. *Fig. 19* show a coniferous society at the summit of a dune. The trees are white pines; the shrubs in front of them, *Juniperus communis;* those at the left, *J. Virginiana*. The grass in the foreground is *Andropogon scoparius*. Coniferous forests on exposed slopes are shown in *figs. 6* and *21*.

The coniferous forests heretofore considered are chiefly on exposed slopes and summits. Sometimes there are coniferous forests farther inland developed on older and lower dunes. The protection here is greater and the air is less xerophytic. Extensive forests of this type were found between Frankfort and Empire and on Beaver island. The trees are chiefly pines or balsams just as before, but the evergreen undergrowth of junipers

and bearberries is largely replaced by such plants as *Vaccinium Pennsylvanicum*, *V. Canadense*, *Epigaea repens*, *Gaultheria procumbens*, *Linnaea borealis*, *Melampyrum Americanum*, *Pteris aquilina*. In the more open and sterile places there is often a moss or lichen carpet, consisting largely of *Cladonia rangiferina* (or other Cladonia species) or *Polytrichum commune*. At the south end of the lake plant societies of this type become more like pine barrens. On the east coast of Beaver island there is a beautiful gradation series from the heath on the beach through a pine forest like that described in this paragraph into a pine forest in which there is almost no undergrowth at all. The scarcity of herbaceous or shrub vegetation is due to the dense shade and the carpet of pine needles. This last type is the summit of the evergreen series, and is in all probability a climax type, at least in certain situations.

A very distinct type of coniferous forest is especially well developed at the south end of the lake. Since it is not developed in exposed situations, or even on old dunes, but in low depressions between dunes, it may be called a pine bottom. These societies are developed where the soil is almost hydrophytic. A common location for these miniature pine forests is about the gently sloping margin of an undrained swamp. *Figs. 9*, *13*, *14*, and *20* show them in such a situation. The line of demarcation between the sedge swamp and the pines is usually quite sharp. The surface of the soil where the pines grow may be less than a meter above the water level.

The character tree of the pine bottoms is always *Pinus Banksiana*. This species is, perhaps, less common than the white pine at the higher levels, but the white pine is rarely, if ever, present on the bottoms. No growth of trees anywhere in the dune region is so pure as the pine growth here. The most common shrubs in these locations are *Hypericum Kalmianum*, *Salix glaucophylla*, *Arctostaphylos Uva-ursi*, and *Juniperus communis*. *Linnaea borealis*, *Arabis lyrata*, *Fragaria Virginiana*, and species of Pyrola are frequent. The development of the pine bottom floras was seen at several points. One of the most interesting cases

was in a region of oak dunes, where a railroad company had removed considerable sand and lowered the level several meters. Although surrounded on all sides by oaks and at some distance from a pine flora, the new flora at the lower level is developing into that of a pine bottom.

c. The rejuvenated dunes.—The instability of dune conditions is not confined to the dune-complex. The capture or establishment of a dune is liable to be stopped at any point and retrogression toward the active dune conditions instituted. Even a dune that has long been completely established may have its vegetation destroyed and pass again into a state of activity. This process may be called rejuvenation. Any dune may become rejuvenated if the physical conditions are favorable, but the great majority of rejuvenated dunes are developed from established coniferous dunes; hence this type is discussed in connection with the evergreen series. The coniferous forests that develop on the windward slopes near the lake are peculiarly subject to destruction. The slightest change in the physical conditions is often sufficient to bring about the destruction of a coniferous society. The removal of a comparatively slight barrier may be enough to direct the entire wind energy against a pine forest.

The formation of a wind-sweep is, perhaps, the most common way for rejuvenation to begin. *Fig. 6* shows a windward slope tenanted by conifers that has become rejuvenated at three points. One of these wind-sweeps is seen at closer range in *fig. 21*. This latter sweep is forty-five meters in height, and the angle of slope varies from twenty to thirty degrees. When once a sweep is formed the tendency to self-perpetuation becomes greater and greater, since the wind becomes more and more concentrated as the sweep grows deeper. The destruction of the forest vegetation is very soon accomplished at such a place. The desiccating influence of the wind becomes increased and makes it difficult even for the xerophytic conifers to survive. At no place is the destructive action of the sand-blast seen so well as in these rejuvenated sweeps. The branches and even the

trunks of the trees have the softer parts carved away, while the more resistant portions stand out in conspicuous relief. The leaves, especially of deciduous trees, are torn or withered or even altogether destroyed.

These destructive agencies are aided by another force that is altogether irresistible when the sweeps grow deeper, the force of

FIG. 24.—Beginnings of a heath on a fossil beach at North Manitou island. Grasses, sand cherries, and patches of Hudsonia in the foreground. Low Ammophila dune at the center. Patches of bearberry heath forming farther back. Advance of the coniferous forest out upon the heath.

gravity. *Fig. 22* shows a plant society that is being destroyed mainly by gravity. The view is taken looking at the side of a deep gorge-like wind-sweep which the wind has cut. As the wind blows along, its energy increased by concentration, a large amount of sand is picked up along the base of the steep sides. The sand is as steep as it will lie, so that each removal causes a movement of the sand down the slope. The fallen trees shown in the photograph have been overturned and carried down the

slope in just this way. That the direct action of the wind is also powerful enough to destroy without the assistance of gravity is proven by the dead but standing trees at the left, where the action of gravity happens to be much less.

Many plant species resist the process of dune rejuvenation to a surprisingly successful extent. *Fig. 23* shows the last remnant of a plant society that may have been somewhat extensive. The tree at the center is a basswood, a tree which could never develop in such an exposed situation. In all probability this mound is a fragment of a protected lee slope, on which the basswood grew and flourished for a time. The grass at the left is Calamagrostis; the tenacity with which it holds its ground has already been mentioned. Sometimes a group of cedars, *Juniperus Virginiana*, remain at the apex of a conical mound of sand, their associates having been swept away with the sand in which they grew. On the beach at Charlevoix there is a stranded clump of stunted trees of Thuya; they are probably the remnant of a society which has been otherwise destroyed.

As a wind-sweep is developed, and the evergreen vegetation destroyed, many plants that have been previously mentioned as characteristic of bare and exposed situations again make their appearance. The most prominent of these are *Artemisia Canadensis* (or *A. caudata*), *Elymus Canadensis*, *Solidago humilis Gillmani*, *Asclepias Cornuti*, *Œnothera biennis*, *Rosa Engelmanni*, *Calamagrostis longifolia*, *Prunus Virginiana*. In addition to these there come in, of course, the annuals and biennials mentioned in connection with the wind-sweeps on the dune-complex.

While rejuvenated dunes are to be found along the entire coast, they reach their highest development northward, especially at the summit of the terraces and bluffs. Perched dunes, it would seem, are favorably located for destruction by the wind. At Frankfort and Empire the perched dunes are in the earlier stages of rejuvenation. At Glen Haven these dunes have been rejuvenated, the vegetation entirely destroyed, and the sand removed inland to form the gigantic moving dunes previously mentioned. The substratum on which the dunes rested remains

as a bare gravel mesa, with only the Sleeping Bear left to tell the tale of its former occupation by coniferous dunes. It is barely possible that some of these so-called rejuvenated dunes have never been established, and that they have grown slowly to their present height *pari passu* with the vegetation. This is purely a theory without any facts whatever to support it. The evidence

FIG. 25.—Juniper heath on North Manitou island. Young heath patches at the left background. Fully developed heath in the foreground. Advancing coniferous forest at the right background.

seems to point unmistakably to an establishment followed by rejuvenation. Evergreen vegetation is very poorly adapted for any *pari passu* growth, such as is found on the embryonic dunes.

3. *The oak dunes.*

At the south end of the lake, and as far up the eastern shore as Manistee, there may be seen old dunes covered over with rather open and scrubby oak forests. These dunes have long been established and are entirely free from the destructive sand-

laden winds which are so influential in determining the character of the other dune societies. As a rule the oak dunes are low and are separated from the lake by several series of dunes on which the vegetation is less stable.

The dominant tree on the oak dunes is the black oak, *Quercus coccinea tinctoria*.[5] This tree is far more abundant than all others combined. The only other tree that may be called characteristic in the Dune Park region is *Quercus alba*. On some oak dunes there are low trees or tall shrubs of *Sassafras officinale*, *Cornus florida*, *Amelanchier Canadensis*, and *Hamamelis Virginiana*. The characteristic shrubs are comparatively few except along the lower margins toward the swamp level, or on shaded northern slopes. The most abundant shrubs are *Vaccinium vacillans* and *V. Pennsylvanicum*, *Salix humilis*, *Viburnum acerifolium*, *Rosa blanda* and *R. humilis*, and *Rhus copallina*.

The herbaceous vegetation of the oak dunes is very diversified and interesting. The trees are always far enough apart to permit an extensive undergrowth of relatively light-loving plants. On the southern slopes, where there is considerable exposure to the sun, there is rarely a continuous vegetation carpet, but a more or less tufted vegetation with intervening patches of naked sand. A large number of herbs are characteristic of such places, for example: *Pteris aquilina*, *Koeleria cristata*, *Cyperus Schweinitzii*, *Carex Pennsylvanica*, *C. umbellata*, *C. Muhlenbergii*, *Tradescantia Virginica*, *Arabis lyrata*, *Lupinus perennis*, *Tephrosia Virginiana*, *Lespedeza capitata*, *Euphorbia corollata*, *Helianthemum Canadense*, *Viola pedata*, *Opuntia Rafinesquii*, *Œnothera rhombipetala*, *Monarda punctata*, *Aster linariifolius*, *Helianthus divaricatus*. In very open places there are various species of Geaster and Lycoperdon, *Festuca tenella*, *Polygonum tenue*, *Polygonella articulata*, *Talinum teretifolium*, *Mollugo verticillata*, *Draba Caroliniana*, *Linaria Canadensis*, *Krigia Virginica*.

On the shaded northern slopes *Pinus Banksiana* and *Pinus*

[5] The closely related *Quercus rubra* and *Q. coccinea* occur commonly in neighboring plant societies and may be present on the dunes, as may hybrids between any of the three forms here mentioned.

Strobus often occur with the oaks (see *fig. 20*). The undergrowth is often a complete vegetation carpet, and consists of Vaccinium, Viburnum, and others of the above plants, together with many different forms. Among the plants here there may be mentioned various species of Cladonia and Peltigera, several mosses, *Aquilegia Canadensis*, *Epigaea repens*, *Phlox pilosa*.

FIG. 26.—Development of a juniper heath in a pasture at Beaver island.

In the background of *fig. 9* there may be seen several oak dunes. The view was taken in the winter and shows a dominance of oaks, but the scrub pines are scattered here and there on northern slopes or in exposed situations. *Fig. 11* shows the advance of an active dune on the north slope of an oak dune with a wealth of oaks and a few scattered pines. *Fig. 20* is a view looking upon the north slope of an oak dune (taken in winter). The pines are abundant at the base and scattered on the slope. A view of the south slope would show no pines at all.

The conditions for the origin and development of an oak dune flora are obscure. At Grand Haven and Ludington the oak flora appears to follow the basswood flora. Remnants of the basswood flora are conspicuous in both places: Sassafras, Hamamelis, Vitis, Smilacina, *Rhus Toxicodendron*, Smilax, Celastrus. It may be that where the conditions are most favorable a maple forest develops after the basswood, but the oak forest elsewhere. At any rate the maple forests are more prevalent northward and the oak forests southward. While the oak forests at Grand Haven, Ludington, and Manistee are on steep, long-established lee slopes, the oak forests at the south end of the lake are often on rather low ridges, where the basswood may never have prevailed.

Quite probably the pine is the normal predecessor of the oak. The scattered pine trees shown in *figs. 9* and *20* may be the relicts of a more extensive pine flora that has been succeeded by the oaks. The oak cannot get a foothold until the dune has become well established and protected from the lake winds. If the pines are scattered, there is opportunity for the oak seedlings to develop successfully. Forest fires are more destructive to the pines than to the oaks; the former are more readily burned, and basal sprouts are less likely to appear afterward than in the case of the oaks. Near Dune Park there is a tract on which the pines have been burned and replaced by the oaks.

One of the most striking landscape features of the Dune Park region is the appearance of the pines at the lower levels (pine bottoms), and again on the highest summits. The oaks occupy an intermediate position as to altitude. The reason for this distribution seems to be that the pines have a much wider range of life conditions than the oaks. The oaks are excluded from the summits because of the extreme exposure to wind and cold; they are not xerophytic enough for such a habitat. They are excluded from the bottoms, because the conditions are too hydrophytic for them there. The pines are excluded from the intermediate positions not because of lack of adaptation, but because the oaks are better adapted for that position than are the pines.

Where the oaks can live at all, they seem able to drive out the pines, while the pines occupy areas that are not adapted to the oaks.

The flora of the oak dunes, especially that found on sunny southern slopes, is a true xerophytic flora, but a xerophytic flora resembling that of the more southern type, where the adaptations are developed to protect against heat and the excessive transpiration which it causes. The flora on northern and windward slopes is predominantly evergreen, developing into a heath or a coniferous forest. This flora, too, is xerophytic, but of an arctic or alpine type, where the adaptations are developed to protect against the wind and cold and the dangers of excessive transpiration which they bring. The correctness of this view is shown by studying the floras of the oak and pine dunes. The former has a flora related to those farther south, containing Opuntia, Euphorbia, and many other plants of southern range. The pine dunes, on the other hand, show the farthest southern limits of many northern plants—for example, the scrub pine itself. Linnaea, the bearberry, and many others have a northern range.

V. Conclusion.

No attempt will be made to summarize the results of this study, but a few of the more striking phenomena of the Lake Michigan dunes and their vegetation will be given. The dunes have been determined in the main by westerly winds. The great majority of the dunes are established, and many of them are perched high up on bluffs. The vegetation is xerophytic, belonging either to the arctic or desert type.

The xerophytic beaches are subdivided into three zones: the lower beach which is washed by summer waves and is essentially devoid of life; the middle beach which is washed by winter waves and is inhabited only by succulent annuals; the upper beach which is beyond present wave action and is inhabited also by biennials and perennials. There are also fossil beaches and gravel terraces with a flora resembling that of the upper beach, but less xerophytic.

Perennial plants are necessary for any extensive dune formation on the beach, since they alone furnish growing obstacles. Such plants must be pronounced xerophytes and be able to endure covering or uncovering. The most successful dune-formers are *Ammophila arundinacea*, *Agropyrum dasystachyum*, *Elymus Canadensis*, *Salix glaucophylla* and *S. adenophylla*, *Prunus pumila*, *Populus monilifera*. Ammophila and Agropyrum form low dunes that have a large area, because of their extensive rhizome propagation. The Elymus dunes do not increase in area since rhizome propagation is absent. The Salix dunes increase both in area and height, because of extensive horizontal and vertical growth. The Populus dunes are the highest and steepest, since the cottonwoods grow quite tall, but do not spread horizontally.

Small dunes are formed in more protected places by plants that are unable to exist on the beach, or where there is rapid dune formation. Among these secondary dune-formers are Andropogon, Arctostaphylos, Juniperus. Primary embryonic dunes may pass gradually into this second type, as this latter passes into the heath.

The stationary embryonic dunes on the beach begin to wander as soon as the conditions become too severe for the dune-forming plants. The first result of this change is seen in the reshaping of the dune to correspond with the contour of a purely wind-made form. The rapidity of this process is largely determined by the success or failure of the dune-formers as dune-holders. The best dune-holders are Calamagrostis, Ammophila, and Prunus.

There are all gradations between a simple moving dune and a moving landscape; the latter may be called a dune-complex. The complex is a restless maze, advancing as a whole in one direction, but with individual portions advancing in all directions. It shows all stages of dune development and is forever changing. The windward slopes are gentle and are furrowed by the wind, as it sweeps along; the lee slopes are much steeper. The only plant that flourishes everywhere on the complex is the succulent annual, *Corispermum hyssopifolium*,

although *Populus monilifera* is frequent. The scanty flora is not due to the lack of water in the soil, but to the instability of the soil and to the xerophytic air.

The influence of an encroaching dune upon a preexisting flora varies with the rate of advance, the height of the dune above the country on which it encroaches, and the nature of the vegetation. The burial of forests is a common phenomenon. The dominant forest trees in the path of advancing dunes are *Pinus Banksiana*, *Quercus coccinea tinctoria*, and *Acer saccharinum*. All of these trees are destroyed long before they are completely buried. The dead trees may be uncovered later, as the dune passes on beyond.

In the Dune Park region there are a number of swamps upon which dunes are advancing. While most of the vegetation is destroyed at once, *Salix glaucophylla*, *S. adenophylla*, and *Cornus stolonifera* are able to adapt themselves to the new conditions, by elongating their stems and sending out roots from the buried portions. Thus hydrophytic shrubs are better able to meet the dune's advance successfully than any other plants. The water relations of these plants, however, are not rapidly altered in the new conditions. It may be, too, that these shrubs have adapted themselves to an essentially xerophytic life through living in undrained swamps. Again it may be true that inhabitants of undrained swamps are better able to withstand a partial burial than are other plants.

Vegetation appears to be unable to capture a rapidly moving dune. While many plants can grow even on rapidly advancing slopes, they do not succeed in stopping the dune. The movement of a dune is checked chiefly by a decrease in the available wind energy, due to increasing distance from the lake or to barriers. A slowly advancing slope is soon captured by plants, because they have a power of vertical growth greater than the vertical component of advance. Vegetation commonly gets its first foothold at the base of lee slopes about the outer margin of the complex, because of soil moisture and protection from the wind. The plants tend to creep up the slopes by vegetative prop-

agation. Antecedent and subsequent vegetation work together toward the common end. Where there is no antecedent vegetation, Ammophila and other herbs first appear, and then a dense shrub growth of Cornus, Salix, *Vitis cordifolia*, and *Prunus Virginiana*. Capture may also begin within the complex, especially in protected depressions, where *Salix longifolia* is often abundant.

Tilia Americana develops rapidly on the captured lee slopes, and the thicket is transformed into a forest. The trees grow densely, and there is little or no vegetation carpet. Associated with Tilia is a remarkable collection of river bottom plants, so that the flora as a whole has a decided mesophytic cast. These plants have developed xerophytic structures that are not present in the river bottoms. Acer and Fagus succeed Tilia and represent the normal climax type of the lake region, the deciduous forest.

On the established windward slopes the development is quite different from that described above. There is a dominance of evergreens instead of deciduous vegetation. The soil conditions are nearly alike on the two slopes, but the air is more xerophytic on the windward slopes. The evergreen flora starts as a heath formed of Arctostaphylos, *Juniperus communis*, and *J. Sabina procumbens*. The heath arises on fossil beaches, secondary embryonic dunes, or wherever the wind is relatively inactive and where the conditions are too xerophytic for the development of a deciduous flora. Before long the heath passes into a coniferous forest, in which *Pinus Banksiana*, *P. Strobus*, or *P. resinosa* dominate. Coniferous forests also occur on sterile barrens and in bottoms, where the conditions are also unfavorable for deciduous forests. A slight change in the physical conditions may bring about the rejuvenation of the coniferous dunes, because of their exposed situation. Rejuvenation commonly begins by the formation of a wind-sweep; the vegetation on either hand is forced to succumb to sand-blast action and gravity.

The evergreen floras are more and more common northward, while to the south there are developed forests in which *Quercus coccinea tinctoria* prevails. The oak forests are more common on

inland dunes and on southern slopes. The oaks may follow the pines, when the areas occupied by pines become sufficiently protected from cold winds. The pines have a much wider range of life conditions than the oaks, since they appear at lower levels, higher levels, and on northern or windward slopes. The oaks flourish best on southern slopes. The flora of the oak dunes is xerophytic, but of the desert type, while that of the pine dunes is of the arctic xerophytic type. The pine dunes have a northern flora, the oak dunes a southern flora.

VI. Previous studies of sand dune floras.

A great deal of physiographic work has been done in sand dune areas in total disregard of the plant life, although the results obtained from this study show that the vegetation profoundly modifies the topography. In like manner the flora has often been studied from a purely taxonomic standpoint, little attention being paid to the striking effects of the environment upon plant structures. More recently the ecological standpoint has been taken by a number of investigators, particularly to show the influence of the extreme environment upon plant organs and tissues. The second part of this paper will treat this phase of the subject in some detail. Very little previous work has been done on the geographic phase of the subject from the standpoint of historical development and the order of genetic succession of the various dune types. Still less has there been any adequate study of the modifying influence of vegetation upon topography. These latter phases of the subject have given color to the work which has resulted in this paper.

Warming's work on the sand dune vegetation of Denmark stands in the front rank. In his separate publications and in his text-book of ecology, the conditions on the Danish dunes are quite fully stated. The order of succession, speaking broadly, seems to be quite similar to that along Lake Michigan, but there appears to be less diversity of conditions, and the features appear to be developed on a smaller scale. The strand is succeeded by the wandering or white dunes, and these by the established or

gray dunes. Beyond these are sandy fields. Just as along Lake Michigan, the dune floras may pass into the heath and these latter into coniferous forests.

There is a remarkable similarity in the flora of the Danish and Lake Michigan dunes. The same genera and often the same species occur in the two regions. *Cakile maritima* and *Lathyrus maritimus* grow on the strand. *Ammophila arundinacea* (=*Psamma arenaria*), *Elymus arenarius*, and *Agropyrum junceum* grow on the wandering dunes. Where the genera are not common or even nearly related, there are to be found in the two regions plants that have the same life habits. There is thus a striking similarity in the two regions in almost every respect, and that too in spite of the marine conditions in Denmark, as contrasted with the inland fresh-water area in the United States. The life conditions appear to be essentially alike on all dunes, whether marine or not, and there are found not only identical life habits, but even identical plant species.

Warming reports Chlamydomonas on the strand in the same relations as along Lake Michigan. Among the sand-binding plants, Warming and Graebner give an important place to mosses. Along the Lake Michigan dunes, mosses do not appear to any great extent until establishment is nearly complete. On the Denmark coast, the Agropyrum dunes are lower than those formed by Ammophila, just as along Lake Michigan. The Danish dunes have also been studied by Raunkiaer, Paulsen, and Feilberg. Erikson has studied the similar dunes of southern Sweden, Giltay and Massart those of Holland and Belgium.

The dunes on the islands along the German coast have been carefully studied by Buchenau and to some extent by Knuth. Graebner, in his exhaustive work on the North German heath, discusses the origin of the heath on naked dune sand. He gives an important place to algæ and moss protonema, since they precede other vegetation, forming the first humus and causing the sand grains to cohere. It is doubtful if these lower plants are so important as sand-binders along Lake Michigan. Rothert and Klinge have studied the coast vegetation of Russia.

The French dunes have been very carefully studied by Flahault alone and also in association with Combres. Some work has also been done in France by Constantin and Masclef. Willkomm's work in Spain and Portugal, covering a period of nearly fifty years, is very complete and satisfactory. Daveau has worked out the conditions along the coast of Portugal. On these more southern dunes, the plant species resemble those along Lake Michigan less than do those in northern Europe, but the life habits are the same.

The dune flora of South Africa has been touched upon by Thode, that of Chile by Kurtz and Reiche, that of northern Siberia by Kjellman, that of New Zealand by Diels. The tropical dunes of Indo-Malaysia have been studied in detail by Schimper, and are fully discussed in his work on the Indo-Malay strand flora and also in his recent Plant Geography. In the latter work there are several excellent discussions of sand dune vegetation, accompanied by photographs from a number of regions. The tropical dunes have totally different species, but even there the dominant dune-formers are grasses with the same life habits as Ammophila.

Dunes may be formed in deserts and inland regions apart from large bodies of water. Those in the Sahara and in the deserts to the northeastward have been more or less studied. Brackebusch has described dunes in Argentina.

In the United States dunes are common along the Atlantic coast, especially in Massachusetts, New Jersey, North Carolina, and Florida. On the Pacific coast they also occur extensively. None of these marine dunes have been exhaustively studied from the ecological standpoint. One of the best works that has ever appeared on strand floras is that by MacMillan on the shores at the Lake of the Woods. The dune formation is not extensive there, but is most admirably treated. As would be expected, there are many species common to Lake Michigan and the Lake of the Woods. The sand hills in the interior have been studied by Rydberg, Hitchcock, and Pound and Clements. Hill has studied the dune floras about Lake Michigan for many

years, and although he has not written a great deal along ecological lines, he has had the ecological standpoint thoroughly in mind and the author has received from him a number of valuable suggestions.

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